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Neohornibrookella sorrentae (Chapman and Crespin, 1928) and allied ostracod taxa from the Neogene of southeastern Australia: systematic and palaeoceanographical relationships, palaeoecology and palaeobiogeography

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Abstract

Three closely allied shallow marine taxa, *Neohornibrookella sorrentae* (Chapman and Crespin), *Neohornibrookella glyphica* (Neil), and *Neohornibrookella nepeani* sp. nov. are recorded from latest early Miocene to late Pliocene strata in southeastern Australia. These taxa, together with *Neohornibrookella quadranodosa* (Holden) from the Miocene of Midway Island (Northwestern Hawaiian Islands), form a morphologically distinct group of relatively large species (the *sorrentae*-group) within the genus *Neohornibrookella* Jellinek. Latitudinal expansion of the subtropical and warm-temperate climatic belts together with the influence of warm western boundary surface currents associated with the North and South Pacific gyres, are likely to have played key roles in the Miocene dispersal of this species group. Species of the *sorrentae*-group first migrated south from equatorial west Pacific regions into southeastern Australia during the early Miocene, under the influence of the East Australian Current. During three time intervals (i) latest early Miocene, (ii) latest late Miocene and (iii) earliest late Pliocene, forceful pulses of the East Australian Current played a significant role

in propelling the widespread distribution of thermophilic *Neohornibrookella* species across southeast Australian shallow marine realms. During intervening middle and late Miocene times, *Neohornibrookella* species are only sporadically present across the Bass Strait region of southeast Australia, indicating a weaker East Australian Current influence and the cooling influence of coastal upwelling. During the mid early Pliocene *Neohornibrookella* species disappeared from the western Bass Strait region, suggesting the complete exclusion of East Australian Current waters from this region. This was probably due to the counteracting influence of the eastward flowing Zeehan Current (extension of the Leeuwin Current) impinging on the western Bass Strait region. This mid early Pliocene palaeobiogeographical partition in Bass Strait, defined by the distribution of *sorrentae*-group species, is here termed the Bassian Gateway. The two species, *N. sorrentae* and *N. glyphica,* occur concurrently during the mid Miocene in southeast Australia, but are associated with different lithofacies. It is hypothesised that there is a heterochronic evolutionary relationship expressed in the ornament of these two species. The thaerocytherid genera *Neohornibrookella* Jellinek, *Tenedocythere* Sissingh and *Bosasella* Bonaduce are here included in the new ostracod subfamily Tenedocytherinae.

Keywords: Neohornibrookella, Tenedocytherinae, Ostracoda, Neogene, Bass Strait, East Australian Current

1. Introduction

The three southeast Australian Miocene ostracod species *Neohornibrookella sorrentae* (Chapman and Crespin, 1928), *Neohornibrookella glyphica* (Neil, 1994) and *Neohornibrookella nepeani* sp. nov., together with *Neohornibrookella quadranodosa*

(Holden, 1976) from the Miocene of Midway Island (Northwestern Hawaiian Islands), form a morphologically distinctive species group within the genus *Neohornibrookella* Jellinek, 1993 of the cytheroid family Thaerocytheridae Hazel, 1967. This is here designated the *sorrentae* species group. Species within this group have previously been variously assigned to the genera *Hermanites* Puri, 1955, *Tenedocythere* Sissingh, 1972 and *Thaerocythere* Hazel, 1967 (Holden, 1976; McKenzie, 1981; Neil, 1994; Mostafawi, 2002). However, in this study, the morphological characteristics that define the genus *Neohornibrookella* are broadened to include this species group, which it is argued, better reflects phylogenetic and palaeobiogeographical relationships (section 2 and section 5.1). Two other species groups, the *transoceanica*-group, and the *titanikos*-group, are also here included in the genus *Neohornibrookella*. Thaerocytherid species of the genera *Neohornibrookella, Tenedocythere* and *Bosasella* Bonaduce, 1985 are assigned to the new, largely tropical to warm temperate shallow marine subfamily, Tenedocytherinae. Systematic descriptions pertinent to this study are presented in the appendix.

Neohornibrookella (*sorrentae*-group) species first appear in the southeast Australian fossil record in the early Miocene, and disappear in the latest Pliocene. Prior to extinction, there was an apparent strong association with Pacific gyre currents. This association is here used to: (i) evaluate the late Cenozoic confluence history of opposing ocean currents within the Bass Strait region of southeastern Australia, and (ii) delineate spatial and temporal palaeobiogeographical patterns in Neogene marine ostracod distribution across the Bass Strait seaway (section 5).

2. Systematic Relationships

The palaeobiogeographical and palaeoceanographical interpretations presented later in this paper (sections 4.1 and 4.3) directly relate to, and are predicated on the taxonomic definitions of the ostracod genus *Neohornibrookella* and its composite species groups as defined below.

2.1 Neohornibrookella generic concept

Neohornibrookella Jellinek, 1993 was originally erected as a monospecific taxon to accommodate a species from modern coastal waters of Kenya, identified by Jellinek (1993) as *Cythere lactea* Brady, 1866. Jellinek (1993) also regarded *Cythere lactea*, which was originally described from Australian marine waters, as a senior synonym of *Hermanites transoceanica* Teeter, 1975 from the Caribbean. Keyser and Schöning (2000), Mostafawi (2002) and Mostafawi *et al.* (2005) concurred with Jellinek's (1993) synonymy of these two taxa. Jellinek's (1993) concept of the carapace morphology for *Cythere lactea* Brady follows that of Holden (1976). It was Jellinek's (1993) clear intention that *Hermanites transoceanica* Teeter, 1975 be the type species, his nomination of *Cythere lactea* Brady, 1866 as such, being only because he believed the former species name to be a junior synonym of the later species name. However, Whatley *et al.* (2004) and Titterton and Whatley (2008) considered the original hand drawn illustrations of *Cythere lactea* in Brady (1866) to not closely resemble *Hermanites transoceanica* Teeter, 1975. We have examined light microscope images of the syntype specimen of *Cythere lactea* Brady, 1866 (courtesy of David Horne), which is currently housed within the G. S. Brady Collection in the Discovery Museum, Newcastle upon Tyne, United Kingdom. This left valve specimen, is the only type material for *Cythere lactea s.s.* (see also discussion in Titterton and Whatley, 2008). This specimen is of a different species to that represented by the type material of *Hermanites transoceanica* Teeter 1975 (fig. 11 p, r) (D. Horne pers. comm. to MW). The hand drawn illustration of the external left valve of *Cythere lactea* in Brady (1866, pl. 60, fig. 3a) faithfully reproduces the

posterodorsal ridge ornament of this species, which is different to that in *Hermanites transoceanica* as illustrated in Teeter, 1975 (fig. 11 p, r). Despite uncertainty relating to the identity of the type species for *Neohornibrookella*, in this study we have assumed that the valve and carapace features of *Hermanites transoceanica* specimens from Kenyan coastal marine waters, misidentified as *Cythere lactea* Brady, 1866 by Jellinek (1993; pl. 28, figs 436-443), are the primary defining characters for this genus. This view accords with the current consensus concerning the defining carapace characters of *Neohornibrookella* (e.g. Keyser and Schöning, 2000; Mostafawi, 2002 and Mostafawi *et al.*, 2005). A forthcoming publication will provide formal resolution of the type species identity for *Neohornibrookella* - and this taxonomic issue is not further discussed in detail here.

Jellinek (1993) considered the presence of three frontal muscle scars to be a key morphological characteristic of his new genus *Neohornibrookella.* Jellinek's (1993) emphasis on this character as a generic diagnostic feature is reflected by his establishment of a different genus *Paraquadracythere* Jellinek, 1993 to accommodate the species *Cythere deltoides* Brady, 1890, which Jellinek (1993) indicated had two frontal muscles scars. However, Labutis (1977) illustrated three frontal muscles scars in specimens of *Cythere deltoides* from Gladstone Harbour on the Great Barrier Reef, northeast Australia. Thus, there seems to be a degree of intraspecific variability in the frontal muscle scars for this species, and the genus *Paraquadracythere* is, therefore, here regarded as a junior synonym of *Neohornibrookella* (as also suggested by Mostafawi, 2002).

In this study a broad range of species and associated carapace morphologies, are included within *Neohornibrookella.* This is a much broader concept of this genus than originally proposed by Jellinek (1993). Three informal species groups are proposed for

Neohornibrookella, which are differentiated on characteristics of carapace size and ornament as follows:

(i) *Neohornibrookella transoceanica* (Teeter, 1975), *Neohornibrookella deltoides* (Brady. 1890), *Neohornibrookella setigera* (Holden, 1976) and *Neohornibrookella trindadensis* (Coimbra and Carreño, 2012) form the first group, here referred to as the *transoceanica*-group. Within the genus *Neohornibrookella,* these are relatively small to medium-sized species that generally possess two short oblique ribs running across an indistinct subcentral tubercle.

(ii) *Neohornibrookella sorrentae* (Chapman and Crespin, 1928), *Neohornibrookella glyphica* (Neil, 1994), *Neohornibrookella nepeani* sp. nov., and *Neohornibrookella quadranodosa* (Holden, 1976) form the second group here referred to as the *sorrentae*-group. Within the genus *Neohornibrookella* these are relatively large species that have a distinct subcentral tubercle with usually indistinct superimposed ribs.

(iii) *Neohornibrookella titanikos* (Whatley *et al.*, 2000), *Neohornibrookella stasiotes* (Whatley *et al.*, 2004) and *Neohornibrookella alloios* (Whatley *et al.*, 2000) form the third group, here referred to as the *titanikos*-group. Within the genus *Neohornibrookella* these are medium-sized to large species, where the main ridges posterior of the subcentral tubercle join to form a three-sided, broadly sub-triangular, ornamental feature.

Geographical and chronological parameters of these informal species groups are outlined in section 5.1. A further fossil species, *Cythere bavarica* Lienenklaus, 1896 (*sensu* Bonaduce *et al*, 1986), from the Miocene of the Mediterranean may be ancestral to *Neohornibrookella* species.

2.2 Tenedocythere generic concept

The concept of *Tenedocythere* was established by Sissingh (1972) on fossil species from the eastern Mediterranean such as *Tenedocythere prava* (Baird, 1850) (type species) and *Tenedocythere mediterranea* (Ruggieri, 1962). Bonaduce *et al.* (1986) and Mostafawi (2002) extended the number of fossil species assigned to this genus, but all these were also from the Mediterranean region. Holden (1976), McKenzie (1981, 1986), Whatley and Jones (1999), Whatley *et al.* (2000, 2004) and Titterton and Whatley (2008) took a broader view of the range in carapace morphology, including, for instance, *Cythere deltoides* Brady, 1890 and *Hermanites transoceanica* Teeter, 1975, within this genus. In this study the concept of the genus *Tenedocythere* is confined to Mediterranean fossil and Recent species (i.e., *sensu* Bonaduce *et al.*, 1986 and Mostafawi, 2002), which in addition to *T. prava* and *T. mediterranea,* includes *Tenedocythere exornata* (Terquem, 1878), *Tenedocythere scalprata* Bonaduce *et al.*, 1986, *Tenedocythere parallela* Bonaduce *et al.*, 1986, *Tenedocythere cruciata* Bonaduce *et al.*, 1986, *Tenedocythere subulata* Bonaduce *et al.*, 1986, *Tenedocythere perplexa* Bonaduce *et al.*, 1986, *Tenedocythere birestis* Bonaduce *et al.*, 1986, *Tenedocythere obsoleta* Bonaduce *et al.*, 1986, *Tenedocythere scabriuscula* Bonaduce *et al.*, 1986 and *Tenedocythere numerata* (Terquem, 1878). Of further note, Mostafawi (2002) has divided these Mediterranean *Tenedocythere* species into two groups – the *prava* and *exornata* species groups.

2.3 Neohornibrookella and Tenedocythere ontogeny

One common characteristic of *Neohornibrookella* and *Tenedocythere* species is their distinctly bimodal ontogenetic development in carapace morphology. For species of these genera, adult, penultimate and rarely A-2 instars, have a vastly different carapace shape to earlier ontogenetic stages. Early stage instars display a dramatic posterior taper, which gives valves a subtriangular shape in lateral view, whereas late stage juveniles and adults generally

possess a more subrectangular shape. For the *prava* species-group (i.e., *Tenedocythere s.s.*) juvenile forms are illustrated in Bonaduce *et al.* (1986; text-figs 4, 5; pl. 9, figs 5-7). For the *transoceanica* species group (i.e., *Neohornibrookella s.s.*) juvenile forms are illustrated in Keyser and Schöning (2000; pl. 4, fig. 70), Hartmann (1981; pl.6, fig. 2), Whatley *et al.* (2004; pl. 4, fig. 22), and Titterton and Whatley (2008; pl.3, fig.18). The early juvenile stages of species in both these genera are all very similar in carapace shape and exhibit a distinctly different shape in lateral views to corresponding adults. Ontogenetic bimodality in carapace shape is also reflected in the *titanikos*-group (Whatley *et al.* 2004; pl. 5, fig. 17) and *sorrentae*-group (this study; Figs 2-7). Marked bimodality in ontogenetic carapace development led Chapman (1914, 1916) and Chapman and Crespin (1928) to assign different names to early stage instars and adult specimens of *N. sorrentae* (see Fig. 3D and Fig. 7A). The strong bimodality in carapace ontogenetic development, which manifests itself as a sharp switch in shape, is a very conspicuous trait of the genera *Neohornibrookella* and *Tenedocythere.* However, ontogenetic carapace outline bimodality is also common in many other ostracod groups, relating to the earlier ontogenetic development of anterior relative to posterior appendages. Nevertheless, the sharp switch in carapace outline during ontogeny in *Neohornibrookella* and *Tenedocythere* species, coupled with the very similar, and particular overall carapace morphology of early stage instars of species within these genera (see appendix section 1.1.2), probably reflect a close phylogenetic relationship.

Sissingh (1972) originally made *Tenedocythere* a subgenus of *Quadracythere* Hornibrook, 1952 – an understandable view given that both *Tenedocythere s.s.* and *Quadracythere* include many species with a subquadrate carapace with similar internal features. However, one of the common characteristics of *Quadracythere s.s.* species from late Cenozoic temperate shallow seas of Australasia ("type region"), is that adults, late stage juveniles and early stage juveniles

all have very similar carapace / valve shapes (e.g. *Quadracythere truncula* (Brady), *Quadracythere mediaruga* Hornibrook and *Quadracythere biruga* Hornibrook). There is no bimodality in the ontogenetic development of the carapace shape as is so distinctive in Mediterranean *Tenedocythere* species and Pacific *Neohornibrookella* species. The lack of this bimodality in ontogenetic carapace development in *Quadracythere s.s.* species suggests that this genus is not as closely related to *Tenedocythere* as originally inferred by Sissingh (1972).

2.4 Neohornibrookella, Tenedocythere and Bosasella ornament

Despite a probably close phylogenetic relationship, there is a fundamental difference in the shape and external ornament of adult *Neohornibrookella* and *Tenedocythere* species as defined above. Species of *Neohornibrookella* tend to possess a more elongate subrectangular shape than the typically more subquadrate-shaped *Tenedocythere* species. (The subquadrate Pacific *Neohornibrookella* species illustrated by Cronin (1988, pl.1, fig. 8) is one exception to this shape "rule".) More significantly, *Tenedocythere* species nearly always possess a strong posterior ridge that extends vertically from the posterodorsal cardinal angle to the posteroventral cardinal angle, and connects with equally prominent subdorsal and subventral ridges that run parallel to the dorsal and ventral margins respectively. In the posterodorsal region of the carapace, the posterior and dorsal ridges typically unite at an angle of approximately 90° to form a prominent hinge-ear ridge structure (see text-fig. 2 in Bonaduce *et al*, 1986). In species of *Neohornibrookella* this hinge-ear ridge is generally subdued or absent. The more prominent posterodorsal ornament in *Neohornibrookella* species is of weak oblique ridges (or distinctive lines of fossae) that extend from a position adjacent to the subcentral tubercle, to a position near the posterodorsal cardinal angle, terminating in a small posterodorsal node or spine (Fig. 8).

Bosasella Bonaduce, 1985 is another genus that appears to have a close phylogenetic relationship to *Neohornibrookella*. *Bosasella* species also display a distinct bimodality in their ontogenetic carapace development similar to that seen in *Neohornibrookella* and *Tenedocythere* species. However, species of *Bosasella* possess ornament that includes a very particular posterodorsal ridge pattern. This posterodorsal ridge ornament pattern, was termed a "posterodorsal loop" by Benson (1972; fig.9). This feature is ubiquitous in adult *Bosasella* specimens, and is often also evident in juvenile specimens. Species of *Neohornibrookella* lack a distinct posterodorsal loop (e.g. *Neohornibrookella transoceanica* (Teeter 1975)). The species *Bosasella dubia* Jellinek, 1993 possesses a posterodorsal loop but, atypically, also possesses a relatively small carapace and displays suturing of the frontal muscle scars like some *Neohornibrookella* species (see Jellinek 1993, figs 413-420). This suggests that *B. dubia* is a transitional form between these two genera. Given the carapace morphological similarities between some species of these two genera, it is possible that the genus *Neohornibrookella*, as here broadly defined, includes the antecedent or antecedents of *Bosasella* species.

2.5 Hermanites, Jugocythereis and Thaerocythere comparisons

Various species here placed in *Neohornibrookella* have been previously placed in the genera *Hermanites* or *Jugocythereis* (Holden, 1976; Neil, 1994, 2000a, 2002, 2006; Neil and Bell, 2006). *Neohornibrookella* species generally possess two rounded frontal muscles, the lower one often showing evidence of suturing and sometimes becoming fully divided to produce a frontal muscle scar pattern composed of three scars. As mentioned above, in *N. deltoides* this variation is intraspecific. In species of *Hermanites* and *Jugocythereis* from Atlantic and Gulf coasts of the USA (which includes the type locations of the types species for both genera), the frontal muscle scar pattern most commonly includes a J, V or U shaped lower scar

beneath a rounded upper scar. This type of frontal muscle scar is not known in species of *Neohornibrookella* as here defined.

Hazel (1968) described the muscle scar pattern of *Hermanites* Puri, 1955 as follows; "two frontal muscle scars, the upper one rounded and lower one U-shaped, four elongated adductor muscle scars set at back of deep muscle scar pit, the dorsomedian divided" (Hazel, 1968, p. 124). According to Benson (1972), the type species of *Hermanites* – *H. reticulata* (Puri, 1954) from the Miocene of Florida – has an overall divided J-shaped frontal muscle scar consisting of a single round upper scar over a lower U-shaped scar. Some species of the closely allied genus *Jugocythereis* Puri, 1957 from the lower Oligocene of Mississippi illustrated by Jellinek (1993, p. 149, text-fig. 17, 1a-c, 2a-c) have a similar frontal muscle scar pattern, with a single circular upper scar situated above the posterior end of a small V-shaped lower scar (i.e., overall divided J-shaped frontal scar in right valve).

Two broad groups of *Hermanites* species occur within the Palaeocene to Miocene of the US Atlantic and Gulf coast regions. A representative of the first group is *Hermanites* cf. *H. fungosa* Butler, 1963 (*sensu* Benson, 1972; pl. 1, figs 11-12) from the Oligocene of Florida. Benson (1972) regarded this species as the probable immediate antecedent of the *Hermanites* type species – *H. reticulata*. *Hermanites* cf. *H. fungosa* (*sensu* Benson, 1972) possesses a dorsal ridge in both valves that forms part of a faint posterodorsal loop (*sensu* Benson, 1972) that is best developed in left valve specimens. Other *Hermanites* species with a posterodorsal loop include *Hermanites plusculmensis* (Schmidt, 1948) from the Palaeocene of Maryland (Hazel, 1968, pl. 24, figs 5 and 10) and a species recorded as *Jugocythereis*? sp. by Jellinek (1993; p.149, text-fig. 17, 3a-c) from the early Oligocene of Mississippi. *Hermanites paijenborchiana* (Keij, 1957) from the Eocene of France also closely resembles *H.* cf. *H. fungosa* (*sensu* Benson, 1972) in general outline and ornament, including the presence of a

conspicuous left valve posterodorsal loop (although unusually, this species sometimes exhibits an anterior fusion of the two frontal muscles scars; Liebau 1975). A number of species that possess relatively subdued ornamental features, such as surface ridges, might also belong in this first *Hermanites* species group. For instance, the species *Hermanites batequensis* Carreño and Cronin, 1993 from the Eocene of the Pacific coast of Mexico lacks a clear dorsal ridge and posterodorsal loop but is otherwise very similar in general shape and ornamentation to *H.* cf. *H. fungosa* (*sensu* Benson, 1972).

Antecedents of *H.* cf. *H. fungosa* (*sensu* Benson, 1972) and *H. paijenborchiana* may occur among European late Cretaceous species of the genus *Limburgina* Deroo with left valve posterodorsal loop structures, and divided V-shaped frontal muscle scars (Deroo, 1966). These two *Hermanites* species together with *H. plusculmensis* and *H. batesquensis* are here regarded as thaerocytherids that are phylogenetically close to trachyleberid root stock.

Representatives of the second group of *Hermanites* species include *Hermanites rukasi* (Gooch, 1939), *Hermanites claibornensis* (Gooch, 1939), *Hermanites collei* (Gooch, 1939) and *Hermanites dohmi* (Howe and Chambers, 1935) from the Eocene of Louisiana, Alabama, Mississippi and North Carolina (Gooch, 1939; Howe and Chambers, 1935; Krutak, 1961; Swain, 1951, 1952), and *Hermanites gibsoni* Hazel, 1968 and *Hermanites hadropleura* Hazel, 1968 from the Palaeocene of Maryland (Hazel, 1968). All these species have both strong dorsal and ventral ridges. The posterior ends of these ridges are characteristically yoked by a usually conspicuous, sinuous, sub-vertical connecting ridge. Despite the strong dorsal ridge, no posterodorsal loop structure is developed. Antecedents of *H. dohmi* and *H. hadropleura* may include species such as *Limburgina verricula* (Butler and Jones, 1957) from the late Cretaceous of Arkansas (*sensu* Hazel and Brouwers, 1982, pl. 1, fig.7) and *Hermanites (s.l.) sagitta* Bate, 1972 from the mid Cretaceous of Western Australia, the later

possessing a typically trachyleberid undivided V-shaped frontal muscle scar. Thus, species such as *H. collei*, *H. rukasi*, *H. dohmi* and *H. hadropleura* are also here regarded as thaerocytherids that are phylogenetically close to trachyleberid root stock.

The common (although not ubiquitous) *Hermanites* muscle scar pattern of a J, V or U shaped lower scar beneath a rounded upper scar is here regarded as a more primitive feature than the two to three rounded frontal muscle scar pattern found in *Neohornibrookella* species.

Mostafawi (2002) suggested that *Neohornibrookella quadranodosa* (Holden, 1976) may have an affinity with *Thaerocythere* Hazel, 1967. However, species of *Thaerocythere* illustrated by Hazel (1967), Swain (1974) and Benson (1972) all have distinctively convex dorsal and ventral margins, and a well rounded posterior with inconspicuous caudal process, a combination of shape characteristics not apparent in *Neohornibrookella* species.

3. Material and methods

For this study a range of field and borehole samples of Cenozoic strata from across southeastern Australia were examined for fossil *Neohornibrookella* specimens. All these sample locations are listed below according to the relevant sedimentary basin, and all sample locations listed contained fossil ostracod assemblages. Specimens collected from the Port Phillip and Western Port basins of south-central Victoria (Fig. 1) were the principal materials considered for taxonomic and palaeoecological analyses (section 5.2 and appendix). Presence or absence records of *sorrentae*-group specimens from a broader palaeogeographical range, principally from the Gippsland, Bass, Otway and Murray basins (Fig. 1), were used for palaeobiogeographical and palaeoceanographical analyses (section 5.3, section 5.4 and section 5.5). For this later component of the study, the main sample materials examined were from Museum Victoria's "stratigraphic collection", although

individual ostracod specimens were not picked and mounted on microfossil slides. Sample sizes from stratigraphical locations represented in the Museum Victoria "stratigraphic collection" varied considerably, and included (i) 1-2 kg field samples, (ii) 50-500g government borehole samples, and (iii) smaller sediment or microfossil residue samples of various origins stored in small boxes or vials. The accuracy of *sorrentae*-group "absence data" is likely to be variable because (i) rare occurrences of species may not have been detected in small sized samples and / or because of, (ii) insufficient sampling of stratigraphic beds at some study sites. Despite these limitations, we argue that the *sorrentae*-group "presence or absence data" recorded below (section 4) are sufficient to elucidate broad Cenozoic distribution patterns of this species group across southeastern Australia. In addition to the records of *sorrentae*-group ostracods generated by inspection of sample materials, records for a few locations have also been derived from previous studies by Chapman (1916), Chapman and Crespin (1928), Eglington (2006), McHenry (1996), Majoran (1996a,b), McKenzie (1979), McKenzie *et al.* (1990, 1991, 1993), McKenzie and Pickett (1984), Neil (1994, 1997), Whatley and Downing (1983) and Warne (1987, 1989). Where appropriate, corrected or updated age information has been applied to these previous records. Locations for which presence or absence data have only been inferred from previous literature are marked by an asterisk in the lists below (sections 4.1 to 4.7).

Details of sampled rock units and geographical coordinates of sampled sites are incorporated with *sorrentae*-group presence / absence data presented below (section 4). Specimens illustrated in this paper (Figs 2–8) are housed in Museum Victoria under registration numbers NMVP12509, P122639–P122640, P143643–P143657, P305746–P305752, P314962–P314969. The following abbreviations are used for recording species dimensions; L = length; H = height; W= width; LV = left valve; RV= right valve.

4. Results

The locations of the southeast Australian strata from which fossil *Neohornibrookella* species were recorded for this study are referenced by geographical coordinates and also indicated in Fig. 1. Locations of southeast Australian strata from which *Neohornibrookella* specimens are recorded as absent are only recorded by geographical coordinates. Both presence and absence data are recorded with reference to geological age and rock formation data (for details on rock formations see Abele *et al.* (1988)). Data on rock formation depth intervals within borehole and oil well sections referenced here, are recorded in Warne (1993) and Li and McGowran (2000).

Ostracod taxa from the majority of studied sample sites indicate palaeoenvironments of stable, normal marine palaeosalinity. However, a few studied sample sites yielded euryhaline thalassic ostracod taxa, or rarely athalassic ostracod taxa mixed with normal marine ostracod species. The palaeoenvironments of these sites were probably influenced by fluctuating salinity, marginal marine conditions. Of all the stratigraphical locations listed below, only one horizon (Nepean 1 borehole at 178.3m) was found to include a *sorrentae*-group species co-occurring with rare euryhaline ostracod species. However, the sample examined from this stratigraphic location was of a strandline lag deposit, where fossils are likely to be of mixed age and provenance (Warne, 2002). It is, therefore, inferred that *sorrentae*-group species are stenohaline marine taxa. Marginal marine palaeoenvironments unsuitable for *Neohornibrookella* species are common in post Miocene strata of the Bass Strait hinterland in southeast Australia (Warne, 2005; Warne and Soutar, 2012). As a consequence *sorrentae*-group absence data from marginal marine strata are likely to be related to conditions of fluctuating palaeosalinity and are not, therefore, of broader palaeobiogeographical or palaeoceanographical significance. Similarly, some samples

examined (e.g., Fyansford Formation at Fossil Beach, Mornington), may have been deposited in water depths beyond the shallow neritic (inner to middle shelf) habitat range of *sorrentae*-group ostracod species, and are thus irrelevant to *sorrentae*-group biogeographical analysis.

4.1 Port Phillip Basin sample locations

In the Port Phillip Basin of south-central Victoria, *sorrentae*-group specimens were collected from the latest early Miocene to earliest mid-Miocene Batesford Limestone and Fyansford Formation exposed along the upper benches of the southwest face of the "new" Batesford Cement Quarry (Lat. 38.11202° S; Long. 144.28749° E) and from earliest mid-Miocene Fyansford Formation at Western Beach (approx. Lat. 38.138° S; Long. 144.356° E) both localities within the Geelong city precinct; from the early mid-Miocene Fyansford Formation (= Balcombe Clay) exposed at the mouth of Gunyoung Creek near of the township of Mornington (Lat. 38.18999 ° S; Long 145.07099° E); from the latest early Miocene to late Miocene Fyansford Formation and latest late Miocene Black Rock Sandstone (= Sandringham Sands) in the Nepean 1 borehole (= Sorrento Bore) near the township of Sorrento on the Nepean Peninsula (Lat. 38.33644° S; Long. 144.73812° E); from the latest late Miocene Black Rock Sandstone (= Sandringham Sands) exposed in cliffs near Beaumaris (suburb of Melbourne) (Lat. 37.99184° S; Long. 145.04242° E); and from hillside outcrops of the earliest Pliocene Moorabool Viaduct Sand on the east side of the Moorabool River under the railway viaduct on the Geelong-Ballarat rail line (Lat. 38.07364° S; Long. 144.28362° E).

Specimens of *sorrentae*-group species are absent from the late Oligocene Waurn Ponds Limestone exposed along Waurn Ponds Drive, Waurn Ponds (Lat. 38.21134° S; Long. 144.26111° E) and on Pigdons Rd, Waurn Ponds (Lat. 38.20118° S; Long. 144.30563° E); from the latest early Miocene to earliest mid-Miocene Fyansford Formation (= Balcombe

Clay) exposed at Fossil Beach near of the township of Mornington (Lat. 38.24145° S; Long 145.02767° E); from the marginal marine late Pliocene Wannaue Formation in the Nepean 1 borehole near Sorrento on the Nepean Peninsula (Lat. 38.33644° S; Long. 144.73812° E), and from the marginal marine mid Holocene Coode Island Silt near Fishermans Bend, Melbourne (approx. Lat. 37.829° S; Long. 144.901° E).

4.2 Western Port Basin sample locations

In the Western Port Basin of south-central Victoria, *sorrentae*-group specimens were collected from the latest early Miocene to earliest mid-Miocene Flinders Limestone exposed in a coastal bluff at the Back Beach adjacent to a golf course near the township of Flinders (Lat. 38.47946°S; Long. 145.01166°E); from the latest early Miocene to early late Miocene Sherwood Marl in boreholes near the townships of Tyabb (Tyabb 1 Lat. 38.239° S; Long. 145.226° E; Tyabb 22 Lat. 38.304° S; Long. 145.217° E; Tyabb 40 Lat. 38.500° S; Long. 145.243° E) and Koo-wee-rup (Koo-wee-rup 14 Lat. 38.183° S; Long. 145.382° E); from boreholes along the western coastal region of French Island (French Island 7 Lat. 38.290° S Long. 145.304° E; French Island 8002 approx. Lat. 38.300° S Long. 145.283° E) and from the latest late Miocene Warneet Sands (*sensu* Warne, 1993) in the Sherwood 18 borehole near the township of Warneet (approx. Lat. 38.221° S, Long. 145.310° E).

4.3 Gippsland Basin sample locations

In the Gippsland Basin of southeast Victoria, *sorrentae*-group specimens were recorded in the early Miocene Glencoe Limestone in Brock's Quarry near Longford (Lat. 38.1771° S; Long. 147.1297° E); from the middle to late Miocene interval of the Gippsland Limestone in the Lakes Entrance Oil Shaft, near Lakes Entrance; from the latest Early Miocene Wuk Wuk Marl at Skinner's on the northern side of the Mitchell River valley, near Lindenow* (Lat.

37.79502° S; Long. 147.4928° E); from the early late Miocene upper beds of the Bairnsdale Limestone at Drier's on the north side of the Mitchell River valley near Bairnsdale (Lat. 37.80958°S; Long. 147.55991°E); from the late Miocene Tambo River Formation on Moondarra Farm (near "Rose Hill") adjacent to the right bank of the Mitchell River west of Bairnsdale (approx. Lat. 37.82565° S; 147.57000° E); from the early Pliocene Jemmys Point Formation near the end of Ferndale Parade, Lakes Entrance (Lat. 37.85819° S; Long. 147.98839° E) and from the road cut on the Princess Highway adjacent to Bunga Creek, near Lake Entrance (Lat. 37.85154° S; Long. 148.03791° E).

Specimens of the *sorrentae*-group species are absent from the early Miocene Longford Limestone in Dowd's Quarry near Boggy Creek, south of Longford (Lat. 38.18782° S, Long 147.07261° E).

4.4 Bass Basin sample locations

In the Bass Basin, *sorrentae*-group specimens have been recorded from the early late Pliocene Cameron Inlet Formation on Flinders Island in Bass Strait (Lat. 40.04344° S; Long. 148.184° E). Samples are equivalent to the uppermost Cameron Inlet Formation of Quilty *et al.* (2013).

Specimens of *sorrentae*-group species are absent from the early Miocene Fossil Bluff Sandstone occurring near Table Cape, northwest Tasmania (approx. Lat. 40.981° S; Long. 145.732° E).

4.5 Otway Basin sample locations

In the eastern Otway Basin of south-central Victoria *sorrentae*-group specimens have been recorded from the early middle Miocene Yellow Bluff beds along Zeally Bay near Torquay (Lat. 38.33038° S; Long. 144.3276° E). In the western Otway Basin of south-west Victoria

sorrentae-group specimens have been recorded from the early mid-Miocene Muddy Creek Marl present in the north bank of Grange Burn, opposite Henty's House, near Hamilton* (Lat. 37.72366° S; Long. 141.9425° E), and from the early late Miocene Gellibrand Marl along the northwestern shore of Lake Bullen Merri, Camperdown (approx. Lat. 38.238° S; Long. 143.097° E).

Specimens of *sorrentae*-group species are absent from late Palaeocene Pebble Point Formation of the western Otway Basin in coastal cliffs near Princetown, southwest Victoria* (Lat. 38.72956° S; Long. 143.18204° E); late Palaeocene to early Eocene Pebble Point and Dilwyn formations of the La Trobe 1 borehole also near Princetown* (Lat. 38.69424° S; Long. 143.14447° E); late Eocene Browns Creek Clay of the western Otway Basin near Browns Creek, Johanna, southwest Victoria (Lat. 38.76946° S; Long. 143.39426° E); early Oligocene Castle Cove Limestone and early Oligocene Lower Glen Aire Clay of the Otway Basin from Castle Cove, southwest Victoria (Lat. 38.78232° S; Long. 143.4257° E); latest early Oligocene Angahook Formation (*sensu* Reekman in Webb, 1995; Warne *et al*., 2003) of the eastern Otway Basin at Bells Headland near Torquay, south-central Victoria (Lat. 38.37256° S; Long. 144.27713° E); late Oligocene Jan Juc Marl of the eastern Otway Basin at west end of Jan Juc Beach adjacent to Bird Rock near Torquay, south-central Victoria (Lat. 38.34968° S; Long. 144.30266° E); early Miocene Zeally Limestone of the eastern Otway Basin (south-central Victoria) from northeast end of Jan Juc Beach, near Torquay, Victoria (Lat. 38.34671° S; Long. 144.30787° E); and absent from the early middle Miocene Gellibrand Marl from the intersection of Native Hut (Sandy) Creek and Barwon River (Lat. 38.10124° S; Long. 144.1058° E), and early late Miocene Gellibrand Marl from along Warrambine Creek (Lat. 38.11584° S; Long. 144.00686° E), both localities near Inverleigh, south-central Victoria. Specimens of *sorrentae*-group species are also absent from the late

middle Miocene to late Miocene Port Campbell Limestone of the western Otway Basin exposed (i) along the top of coastal cliffs at west end of Bay of Islands, Port Campbell, southwest Victoria (Lat. 38.5783° S; Long. 142.8168° E), (ii) along the lower coastal cliffs, Bay of Islands, Port Campbell (Lat. 38.58102° S; Long. 142.82841° E), (iii) near the Sherbrook River, Port Campbell (Lat. 38.6432° S; Long. 143.0571° E), (iv) along the base of cliffs just west of mouth of Curdies Inlet, Peterborough, southwest Victoria (Lat. 38.6095° S; Long. 142.879° E, (v) at The Amphitheatre, Port Campbell (Rutledge Creek Member) (Lat. 38.64133° S; Long. 143.05553° E), and (vi) along the base of cliff at Rutledge's Creek, Port Campbell (Rutledge Creek Member) (Lat. 38.64005° S; Long. 143.5110° E). Further, *sorrentae*-group specimens are absent from the late Miocene Goodwood Formation of the western Otway Basin from Spring Creek near Minhamite, western Victoria (approx. Lat. 37.9987° S; Long. 142.4229° E); early Pliocene Grange Burn Formation of the western Otway Basin from exposures (i) along Forsyth's Bank on Grange Burn, near Hamilton, western Victoria (Lat. 37.7281° S; Long. 141.9457° E), (ii) along MacDonald's Bank on Muddy Creek near Hamilton, western Victoria (Lat. 37.74435° S; Long. 141.93926° E), and from Clifton Bank on Muddy Creek near Hamilton, western Victoria (Lat. 37.73809° S; Long. 141.93070° E); from the normal marine early Pliocene lower Whalers Bluff Formation, and marginal marine late Pliocene upper Whalers Bluff Formation exposed in coastal cliffs near Portland (Lat. 38.32269° S; Long. 141.59990° E); from the early Pleistocene lower Werrikoo Limestone of the western Otway Basin near the mouth of Limestone Creek, west bank of Glenelg River, north of Dartmoor, western Victoria (Lat. 37.7798° S, Long. 141.2325° E), and from the mid-late Pleistocene marginal marine Port Fairy Calcarenite near Goose Lagoon, Port Fairy*, western Victoria (Lat. 38.3825° S; Long. 1421638° E).

4.6 Murray Basin sample locations

In the Murray Basin of south east Australia, *sorrentae*-group specimens have been recorded from the latest early Miocene Lower Morgan Limestone (= Glenforslan Formation), and early mid-Miocene Cadell Marl and Upper Morgan Limestone (= Bryant Creek Formation) from the Murray River cliffs south of Morgan, eastern South Australia (Lat. 34.05384° S; Long. 139.68838° E); Miocene Murray Group in the Mallee Bore 11 from near Murrayville, northwest Victoria (approx. Lat. 35.269° S; Long. 141.181° E) and from the latest Miocene Bookpurnong Formation of the Murray Basin in the Loxton Drainage Shaft No. 18 near the township of Loxton, South Australia (approx. Lat. 34.402° S; Long. 140.601° E).

Specimens of *sorrentae*-group species are absent from the early Miocene Mannum Formation of the Murray Basin at Shell Hill near Wongulla, eastern South Australia (approx. Lat. 34.7° S; Long. 139.56° E).

4.7 Other sample locations

Additional specimens from outside southeast Australia were recorded from the late Pliocene Roe Calcarenite of the Eucla Basin, southern Western Australia (Lat. 31.95081 °S; Long. 127.5773° E).

Specimens of *sorrentae*-group species are absent from the late Eocene Blanche Point Formation and early Oligocene Port Willunga Formation exposed near Blanche Point* (approx. Lat. 35.246° S; Long. 138.462° E) and Port Willunga* (Lat. 35.255° S; Long. 138.461° E); also from the Late Eocene Blanche Point Formation and late Oligocene to early mid-Miocene Port Willunga Formation in the WLG 38 bore* (approx. Lat. 35.307° S; Long. 457° E); WLG 40 bore* (approx. Lat. 35.279° S; Long. 138.461°E) and WLG 42 bore* (approx. Lat. 35.235° S; Long. 138.531° E) near Willunga. All these Blanche Point

Formation and Port Willunga Formation localities occur within the St Vincent Basin, South Australia.

Specimens of *sorrentae*-group ostracods are also absent from the normal marine, mid-late Pleistocene Gundurimba Clay at the "coral locality" near Evans Head*, New South Wales north-coast (approx. Lat. 29.0964° S; Long. 143.3833° E), and from the marginal marine Gundurimba Clay in borehole WRC 39140 near South Gundurimba*, northeast New South Wales (approx. Lat. 28.8908° S; Long. 153.2928° E).

5. Discussion

5.1 Palaeobiogeography of Neohornibrookella species groups

Teeter (1975) was the first to elucidate the essentially equatorial Indo-Pacific and Caribbean distribution of *Neohornibrookella* (*transoceanica*-group) species. Cronin (1988) recognised that the main locus of Recent and fossil *transoceanica*-group distribution was the western Pacific Ocean. Cronin (1988) also discussed possible mechanisms that might account for the wide distribution of *N. transoceanica*, and concurred with Teeter (1973) that the most probable means of migration for shallow marine Ostracoda that inhabit macrobenthic algae, was via drifting seaweed, enabling easy dispersal across deep ocean waters. Bonaduce *et al.* (1980), Whatley (1987), Titterton and Whatley (1988), Jellinek (1993), Whatley and Roberts (1985), Whatley (2000) and Coimbra and Carreño (2012) noted additional records of this species group from the equatorial Indian Ocean, Red Sea, South Pacific Ocean and subequatorial waters of the southwest Atlantic coast (Fig. 9A). The earliest fossil records for this species group include Miocene to Pleistocene occurrences on Enewetak Atoll (Marshall Islands) in the equatorial North Pacific (Cronin, 1988), and early Miocene occurrences on Midway Island (Northwestern Hawaiian Islands) in the mid North Pacific (Holden, 1976).

Neohornibrookella species of the *titanikos*-group are currently known to exist only in modern coastal seas around Henderson, Oeno and Easter islands in the south-east Pacific Ocean (Whatley and Jones, 1999; Whatley *et al.,* 2000, 2004) (Fig. 9B). This group likely owes its origins to the dispersal of an antecedent species from the west Pacific via the South Pacific Ocean gyre. This migration is presumed to be of late Cenozoic age because of the relatively young geological ages of these islands.

Neohornibrookella species of the *sorrentae*-group are currently known only from fossil records. These occurrences include mid-latitude Miocene and Pliocene strata of southern Australia and Northwestern Hawaiian Islands (Fig. 1 and Fig. 9C), a distribution that implies association with Pacific Ocean western boundary currents. Early occurrences of *sorrentae*-group ostracods across southeastern Australia are closely associated with the influx of South West Pacific tropical and subtropical benthic foraminifera into mid latitudes during warm early to mid Miocene climatic phases (Carter, 1985; McGowran *et al.,* 2000). This migration pattern appears to be associated with an early Miocene intensification of the East Australian Current (Eberli *et al*., 2010) and latitudinal expansion of warm climate belts. Neogene shallow marine ostracod faunas of northeast Australia and Papua New Guinea have not yet been described in detail, possibly accounting for the lack of fossil *sorrentae*-group records in equatorial regions of the South West Pacific, although possible descendant groups, such as some *Bosasella* species, are common in present day equatorial and subequatorial regions of the Indian and West Pacific oceans (Jellinek, 1993).

There are four significant biogeographical ocean gateways that have influenced the distribution of *Neohornibrookella* species through time (Fig. 9). The first is the Tethyan Ocean Gateway. The Miocene tectonic driven closure of this biogeographical gateway (Karami *et al.,* 2011) isolated Mediterranean *Tenedocythere* species from Indo-Pacific

Neohornibrookella species, and prevented the migration of the latter into the Mediterranean Sea. The second is the Indonesian Throughflow. During the early Cenozoic this was a broad deep marine seaway, which narrowed during the late Cenozoic due to tectonic collisions between Australia and South East Asia (Cane and Molnar, 2001; Karas *et al.*, 2009). This appears to have generated shallow marine pathways along which *Neohornibrookella* species migrated from the equatorial Southwest Pacific Ocean into the equatorial Indian Ocean and Red Sea. The third is the Bassian Gateway, which marks a late Cenozoic confluence of opposing ocean currents in the southeastern Australian region (see section 5.3.2 for further discussion). The fourth is the Isthmus of Panama, which was open until at least the earliest Pliocene (Fedorov *et al.*, 2013), allowing the spread of *Neohornibrookella* species from the Pacific Ocean into the Caribbean Sea (Cronin, 1988), and subequatorial southwest Atlantic Ocean (Coimbra and Carreño, 2012).

5.2 Morphological variation and palaeoecology

Neohornibrookella species appear to exhibit a degree of phenotypic plasticity. This includes ecophenotypic variation involving the allocation of relatively more calcite for increased valve and ornament thickness, at the expense of carapace size, in high energy (rough) shallow marine environments with carbonate or quartz sand substrates. Conversely in deeper quieter shelf waters with finer grained silt and mud substrates, relatively less calcite appears allocated to the development of shell and ornament thickness, with resultant larger carapaces. This ecophenotypic response to environmental conditions may also be coupled with a degree of heterochronic variation in carapace form. The analyses of species morphological variation and palaeoecology presented below (sections 5.2.1 to 5.2.4) relate to specimens collected from the Port Phillip and Western Port basins.

5.2.1 Neohornibrookella sorrentae

Three morphotypes are here recognised for the species *Neohornibrookella sorrentae* (Chapman and Crespin, 1928). The largest morphotype of *N. sorrentae* (*morphotype 1*) possesses a straight dorsal margin and a subtriangular shaped carapace in lateral view in adult specimens (Figs 2A-F; 7R). These shape characteristics have a juvenile aspect, which in this morphotype appears to be maintained into adult specimens. *Morphotype 1* also displays minimal differential thickening of muri, which do not develop into distinct ridges in the posterodorsal region of the carapace surface. Early stage instars of this morphotype tend to display only very faintly developed reticulate ornament across the carapace surface (Fig. 7A, D). *Morphotype 1* (Fig. 2A-F) is the deepest water variant of *N. sorrentae* (Fig. 10) being found in middle to earliest late Miocene mid-shelf mud facies of the Fyansford Formation in the Nepean 1 borehole (438.9 m – 259.1 m) (Warne, 1993). This mid-shelf morphotype of *N. sorrentae* is commonly associated with the following ostracod taxa: *Bradleya praemckenziei* Whatley and Downing, 1983, *Cytherelloidea intermedia* (Chapman and Crespin, 1928), *Uroleberis minutissima* (Chapman, 1926), *Cletocythereis caudispinosa* (Chapman and Crespin, 1928), *Krithe nitida* Whatley and Downing, 1983, *Neonesidea australis* (Chapman, 1914), *Cytherella* sp., *Australoecia* sp., *Trachyleberis* sp., *Callistocythere* sp., *Occulocytheropteron* sp. and *Cytheropteron* sp.

Morphotype 2 (Fig. 3A-D) is also a relatively large variant of *N. sorrentae*, but possesses a slightly concave dorsal margin and a subrectangular shaped carapace in lateral view in adult specimens (Figs 3A-D; 7S). *Morphotype 2* displays some differential thickening of muri to form ridges in the posterodorsal region of the carapace surface. *Morphotype 2* has a palaeo-bathymetric range intermediate between that of *morphotypes 1* and *3* (Fig. 10). *Morphotype 2* has been found in early to middle Miocene inner shelf marl facies of the Fyansford Formation near Geelong, and late Miocene mid-shelf muddy sand facies of the Fyansford

Formation in the Nepean 1 borehole (240.2 m – 184.4 m) (Warne, 1993). *Neohornibrookella sorrentae* (*morphotype 2*) is commonly associated with the ostracod taxa *Bradleya praemckenziei, Krithe nitida, Pterygocythereis velivola* (Brady, 1880), *Cytherelloidea auricula* (Chapman, 1914), *Cytherelloidea intermedia, Loxoconcha australis* Brady, 1880, *Cletocythereis caudispinosa, Hornibrookella thomasi* (Neil, 1994), *Alataleberis miocenica* McKenzie and Warne, 1986, *Bythocypris subrectangulata* Warne, 1990, *Trachyleberis* sp., *Quasibradleya* sp., *Callistocythere* sp., *Loxoconcha* sp., *Cytherella* sp., *Occulocytheropteron* sp., *Haniaceratina* sp., *Kangarina* sp., *Australoecia* sp., *Cytheralison* sp. and *Dumontina* sp.

Morphotype 3 (Fig. 4A-F) is the smallest variant of *N. sorrentae.* Like *morphotype 2*, adult specimens of *morphotype 3* possess a concave dorsal margin and subrectangular shaped carapace in lateral view. *Morphotype 3* specimens displays significant thickening of muri to form ridges across the dorsal region of the carapace. *Morphotype 3* is the shallowest water form of *N. sorrentae* (Fig. 10) being found in late early Miocene to early mid-Miocene inner shelf (marl and calcarenite facies) of the Batesford Limestone and Fyansford Formation near Geelong, and inner shelf (calcarenite and calcilutite facies) of the Flinders Limestone, near Flinders. *Neohornibrookella sorrentae* (*morphotype 3*) is commonly associated with the following ostracod species: *Hornibrookella thomasi*, *Neonesidea fredericki* Warne, 1988, *Bairdoppilata fyansfordensis* Warne, 1988, *Bradleya lungalata* McKenzie *et al*, 1991, *Hornibrookella nuda* (McKenzie *et al*, 1991), *Neohornibrookella glyphica* (Neil, 1994), *Bythocypris subrectangulata*, *Neobuntonia batesfordiensis* (Chapman, 1910), *Quadracythere* sp., *Trachyleberis* sp., and during the latest early Miocene, the warm water benthic foraminiferan *Lepidocyclina howchini* (Chapman and Crespin, 1932).

5.2.2 Neohornibrookella glyphica

Specimens of *Neohornibrookella glyphica* are typically found in shallow marine calcarenite and calcilutite and calcareous sand facies (Fig. 10). Some adult and late stage juvenile specimens from calcareous sand facies exhibit coalescence of fossae in the anterodorsal region of the carapace. This feature is apparent in the holotype of *N. glyphica* illustrated by Neil (1994; pl. 7, fig. 3). Within this species, variation in the prominence of the subcentral tubercle has also been noted. *Neohornibrookella glyphica* has been recorded from two time intervals - late early Miocene to early mid-Miocene (Batesfordian – Balcombian), and latest Miocene to earliest Pliocene (Cheltenhamian). Late early Miocene to early mid-Miocene strata containing this species include the Batesford and Flinders limestones. Latest Miocene to earliest Pliocene strata containing this species include the Black Rock Sandstone, Moorabool Viaduct Sands and Warneet Sands. In late early Miocene to early mid-Miocene strata, *N. glyphica* is commonly associated with the following ostracod species: *Hornibrookella thomasi, Spinobradleya nodosa* Neil, 1994, *Neobuntonia batesfordiensis, Bairdoppilata fyansfordensis, Neonesidea fredericki, Quadracythere* sp., and *Xestoleberis* sp.; as well as with the warm water benthic foraminiferan *Lepidocyclina howchini* (Chapman and Crespin, 1932). In latest Miocene to earliest Pliocene strata *N. glyphica* is commonly associated with the ostracod species *Ponticocythereis militaris* (Brady, 1866), *Novoloxocythere pileus* Warne, 2004, *Actinocythereis tetrica* (Brady, 1880), *Loxoconcha australis*, *Keijia* sp., *Callistocythere* sp., *Dentibythere* sp., *Baltraella* sp., *Quasibradleya* sp., *Mackencythere* sp., *Australimoosella* sp. and *Xestoleberis* spp.

5.2.3 Neohornibrookella nepeani

Neohornibrookella nepeani has been found within latest Miocene glauconitic and ferruginous shelly sands (Fig. 10) occurring in the Nepean 1 borehole at 178.4 m (basal Black Rock Sandstone). This unit includes rounded and polished shell and vertebrate bone fragments

mixed with pristinely preserved inner shelf (common) and estuarine (very rare) Ostracoda (Warne, 2002). The depositional environment is interpreted as having been a protected, shallow, but open normal marine embayment in close proximity to an estuary (Warne, 1993; 2002). No variation in adult morphology of this species is here recorded, largely due to the limited number of specimens available for study. *Neohornibrookella nepeani* is associated with the following ostracod species: *Cletocythereis curta* McKenzie 1967, *Actinocythereis tetrica, Novoloxocythere pileus, Novoloxocythere kerryswansoni* (Yassini and Jones, 1995), *Kotoracythere hingstoni* (McKenzie *et al.*, 1990), *Loxoconcha australis, Maddocksella tumefacta* (Chapman, 1914), *Neobuntonia* sp., *Pokornyella* sp., *Keijia* sp., *Cytherella* sp., *Callistocythere* sp., *Neonesidea* sp., *Arculacythereis* sp., *Tasmanocypris* sp., *Cytheralison* sp., *Xestoleberis* sp. and rare specimens of *Osticythere baragwanathi* (Chapman and Crespin, 1928) (see also introductory comments for section 4).

5.2.4 Heterochronic polymorphism and speciation

For *N. sorrentae*, different intraspecific morphotypes have different palaeoecological tolerances within Miocene strata of the Port Phillip and Western Port basins (Fig. 10). One difference between these morphotypes is the degree to which muri are thickened and develop into ridges, particularly within the posterodorsal region of the carapace. For various cytheroid species, Neil (2002) has argued that intraspecific differences in mural thickness are an ecophenotypic (non genetic) physiological response to variations in prevailing physio-chemical conditions during carapace formation (i.e., phenotypic plasticity).

The largest morphotype of *N. sorrentae* (*morphotype 1*) has the least thickening of its muri, and appears to be the most fragile of the three *N. sorrentae* morphotypes. The mid-shelf sea floor habitat of *morphotype 1*, being relatively unaffected by wave agitation, seemingly precluded the requirement for particularly heavy calcification of the carapace. The smallest

morphotype of *N. sorrentae* (*morphotype 3*) has the greatest degree of mural thickening, and appears to be the most robust of the three *N. sorrentae* morphotypes. The inner shelf sea floor habitat of *morphotype 3* would have been substantially influenced by wave agitation, so relatively heavy calcification of the carapace would have been an advantage in this high energy marine environment.

While the basic pattern of potential ridging that may develop in adult instars of *N. sorrentae* is likely fixed, variations in muri thickening and ridge development within *N. sorrentae* can cause some minor distortions in adult fossal patterns, which are here regarded as ecophenotypic in nature, consistent with the view of Neil (2002). However, at the deepest water end of its range, adult specimens of *N. sorrentae* (*morphotype 1*) exhibit a quasi-juvenile subtriangular carapace shape. (Compare adults of *morphotype 1* in Fig. 2 A-F with adults of *morphotype 3* in Fig. 4A-F and juveniles in Fig. 7A-E.) Only one of the three *N. sorrentae* morphotypes - *morphotype 1* – maintains a juvenile-like valve shape in the adult instar. Subtriangular shaped adult valves of *N. sorrentae* (*morphotype 1*) also possess straight dorsal margins (Figs 2B, D; 7R), whereas subrectangular shaped adult valves of *N. sorrentae* (*morphotypes 2* and *3*) possess sinuous dorsal margins (Figs 3A, C; 4B, C; 7S). These lateral shape characteristics appear to be either present or absent in adult instars, without intermediaries, suggesting that these intraspecific variations in *N. sorrentae* carapace shape may have a heterochronic basis. Variations in size also tend towards bimodality (i.e., not gradational) with *N. sorrentae morphotype 3* adult valves usually being smaller than *morphotype 1* or *morphotype 2* adults valves (see dimensions data in the appendix). All these observations together suggest that both heterochronic and ecophenotypic factors contribute to intraspecific variation within this group of ostracod species. Of further note, in the species *Neohornibrookella glyphica* (Neil, 1994), the carapaces of A-1 juvenile specimens (Fig. 5F)

broadly resemble those of adult specimens of *N. sorrentae* from the shallower water end of its range (i.e., *morphotypes 2* & *3*; Figs 3D, 4D respectively). Thus it may be that there is a species-level heterochronic evolutionary relationship between *N. sorrentae* and *N. glyphica*.

Overall the intraspecific morphological differences between the three morphotypes of *N. sorrentae* are small compared to the more disjunct differences in adult carapace morphology between the three *Neohornibrookella* species illustrated in this study (i.e., *N. sorrentae, N. glyphica* and *N. nepeani*). We have used these contrasting degrees of morphological difference to distinguish between intraspecific variation and interspecific divergence in carapace form. Disjunct carapace morphological differences between *N. sorrentae, N. glyphica* and *N. nepeani* include differences in adult subcentral tubercle development (Fig. 4 and Fig. 5), large differences in adult valve lateral outline shape (Fig. 4, Fig. 5 and Fig. 6), and large differences in primary adult posterodorsal ridging patterns on the lateral carapace surface (Fig. 4, Fig. 5, Fig. 6 and Fig. 8). For detailed descriptions of the carapace morphology of these three species – see appendix.

5.3 East Australian Current Tracers

The known distribution of the *sorrentae*-species group suggests Miocene dispersal via warm western boundary surface currents associated with the North and South Pacific gyres, although no Miocene occurrences have, as yet, been recorded from the little studied Miocene equatorial or subequatorial faunas of the southwest Pacific and northeast Australia. Fluctuations in the east-west distribution of *sorrentae*-group Ostracoda across southeast Australia during the Neogene (Fig. 1), are here interpreted as reflecting oscillations in the influence of opposing east-west surface ocean currents across the Bass Strait seaway (section 5.3.2). At the present day, the East Australian Current, a western boundary current of the South Pacific Gyre, flows southward down the entire east Australian continental margin,

mixing with eastern Bass Strait waters. Lawver and Gahagan (2003) regarded the mid Miocene tectonic collision between Australia and New Guinea, and associated restriction of equatorial transport of water from the Pacific to the Indian oceans, as a major influence on the flow of surface ocean currents adjacent to the eastern continental margins of Australia and Asia. Broadly consistent with this view, Eberli *et al* (2010) recorded the significant presence of the East Australian Current along the Marion Plateau off the east coast of Queensland, from the latest early Miocene. These findings parallel the views of McGowran *et al.* (2000) concerning the widespread influence of this surface ocean current across southeast Australia during the Mid Miocene Climatic Optimum, as evidenced by southerly latitudinal migrations of tropical larger benthic foraminifera. Of note, however, Gourley and Gallagher (2004) had a somewhat different interpretation for the environmental drivers underpinning mid Miocene southerly migrations of thermophilic benthic foraminifera, arguing that climatic warming and associated latitudinal expansion of tropical and subtropical climate belts was of greater significance than ocean currents.

The modern Leeuwin Current originates in the region of the Indonesian Throughflow and strengthens as it flows southwards, under the influence of the Eastern Gyral Current, down the west Australian coastline. After rounding Cape Leeuwin, the southernmost headland in Western Australia, it flows eastwards along the southern Australian continental margin into the Great Australian Bight. The easternmost extension of the Leeuwin Current is known as the Zeehan Current, which, at the present day, impinges on the western Bass Strait margin before flowing southeastwards down the west coast of Tasmania. Li and McGowran (1994) have suggested that a proto-Leeuwin Current existed in the late Eocene, while Gallagher *et al.* (2009) argued for a Plio-Pleistocene inception. James *et al.* (2006) indicated evidence for a warm Leeuwin Current along the southern coastline of Western Australia during the late

Pliocene. During the Miocene to mid Pliocene, fluctuations in Indo-Pacific surface ocean currents occurred against a backdrop of periodic broad scale oceanic heat (Hornibrook, 1990; Flower and Kennett, 1994; Ravelo, 2010; LaRiviere *et al.*, 2012).

Fossil ostracod data presented here indicates that (i) the significant influence of the East Australian Current across the Bass Strait region of southeast Australia extended beyond the Mid Miocene Climatic Optimum (section 5.3.2), and (ii) there was a significant zone of confluence between the opposing East Australian and Zeehan currents in the western Bass Strait region during the mid early Pliocene (Kalimnan), which formed an important biogeographical gateway (section 5.3.2).

5.3.1 First appearance of the sorrentae-group in SE Australia

The earliest previously recorded occurrence of the *sorrentae*-group in southeast Australia was from the latest early Miocene Muddy Creek Marl of Western Victoria (Neil, 1994). No specimens of this species group have as yet been recorded from Palaeocene to Oligocene shallow marine strata of southern Victoria (McKenzie *et al.*, 1991, McKenzie *et al.*, 1993, Neil, 1997 and Eglington, 2006).

To further define the first appearance of the *sorrentae* group in southeast Australia, the ostracod faunas from several late Oligocene to early Miocene calcarenite, calcilutite and marl lithostratigraphical units in the Geelong, Torquay and Longford districts of southern Victoria, were examined in detail (section 4.1, section 4.3, section 4.5). In the Geelong and Torquay districts of south-central Victoria (eastern Otway Basin), no *sorrentae*-group specimens were found within the late Oligocene (Chattian / Janjukian) Waurn Ponds Limestone or the early Miocene Zeally Limestone (section 4.1 and section 4.5). Of particular note, the lower eight metres of the Zeally Limestone in coastal cliff exposures towards the northeast end of Jan Juc

Beach, near Torquay (Beach Access Point 77w: Lat. -38.34671° S; Long. 144.30787° E) contain sporadically abundant and diverse normal shallow marine ostracod faunas, which conspicuously lack specimens of *Neohornibrookella* spp. Associated planktonic foraminiferid faunas include *Globigerinoides trilobus* (FAD - 23.73 Ma; Wade *et al.*, 2011), but lack *Praeorbulina sicanus* (FAD – 16.40 Ma; Wade *et al.*, 2011), indicating an early Burdigalian / late Longfordian age. In the nearby "new" Batesford Cement Quarry, near Geelong, *Neohornibrookella* spp. become a common component of ostracod faunas in the upper Batesford Limestone (section 4.1), where they are associated with foraminiferid faunas that variably include the planktonic species *Praeorbulina sicanus* and the subtropical benthic species *Lepidocyclina howchini.* This microfaunal association occurs prior to the appearance of the planktic foraminiferan *Praeorbulina glomerosa* (FAD – 16.29 Ma; Wade *et al.*, 2011) within the overlying Fyansford Formation exposed in the southwest face of the "new" Batesford Cement Quarry (Warne, 1993). In the Longford district of southeastern Victoria (Gippsland Basin), specimens of *sorrentae*-group Ostracoda are similarly widespread in latest early Miocene (Batesfordian) to early mid-Miocene marine strata (e.g. Wuk Wuk Marl exposed in the Mitchell River valley, East Gippsland). However, arguably slightly earlier Miocene records occur in this region, such as in the early Miocene Glencoe Limestone in Brock's Quarry near Longford (section 4.3), which Gallagher and Holdgate (1996) indicated was mid early Miocene (late Longfordian) in age. This suggests that a weak East Australian Current initially influenced the eastern Bass Strait region during the mid early Miocene (Burdigalian / late Longfordian), although the more widespread migration (acme) of *Neohornibrookella* (*sorrentae*-group) spp. across southeastern Australia occurred during the latest early Miocene (latest Burdigalian / Batesfordian; Fig. 11 and Fig. 12A).

5.3.2 Palaeo-East Australian Current, the Bassian Gateway, and the Zeehan Switch

As noted above (section 5.3), in southeast Australia, latest early Miocene (latest Longfordian-Batesfordian) occurrences of *sorrentae*-group species are associated with the influx of tropical, southwest Pacific benthic foraminifera. It is on the basis of this indirect evidence, together with the west Pacific ocean gyre distribution of *sorrentae*-group Ostracoda, that southeast Australian occurrences of this ostracod species group are inferred to be linked with the East Australian current waters. However, unlike the tropical foraminiferan *Lepidocyclina howchini* (Chapman and Crespin) and *Cycloclypeus carpenteri* Brady, *Neohornibrookella* (*sorrentae*-group) species continued to sporadically inhabit shallow marine realms of the Bass Strait region throughout much of the middle Miocene (Balcombian) to early late Pliocene (section 4; Fig. 11). This is interpreted to reflect a persistent mid Miocene to Pliocene influence of East Australian Current waters in this region. In southeastern Australia, the palaeogeographical range, biodiversity and abundance of *sorrentae*-group Ostracoda in shallow marine realms, was highest during two small time intervals – the latest early Miocene to early mid-Miocene (Batesfordian- Balcombian), and the latest late Miocene (early Cheltenhamian) (Fig. 11). Both these short time intervals are thus inferred to indicate relatively warm seas associated with (i) mid latitudinal expansions of the southern hemisphere subtropical climate belt, and (ii) particularly strong pulses of East Australian Current waters across southeastern Australia. Within the Port Phillip and Western Port basins, this is reflected by maximum abundances and diversities of *sorrentae*-group Ostracoda during both these time intervals as evidenced by occurrences in the latest early to mid Miocene upper Batesford Limestone and lower Flinders Limestone, and within the latest Miocene basal Sandringham Sand and basal Warneet Sands (section 4.1 and section 4.2; Fig. 11; Warne, 1993, 2005). A similar pattern of bimodal Miocene marine warmth was recorded in the planktonic foraminifera succession of the offshore Gippsland Basin by Gallagher *et al.*, (2001). *Neohornibrookella* (*sorrentae*-group) species are known to extend as far east as

Bairnsdale in southeast Victoria (Wuk Wuk Marl), and at least as far west as Hamilton in SW Victoria (Muddy Creek Marl) and Morgan in eastern South Australia (Morgan Limestone / Cadell Marl) during the latest early Miocene to earliest middle Miocene (Batesfordian-Balcombian); and as far east as Lakes Entrance in southeast Victoria (Jemmys Point Formation) and as far west as Loxton in eastern South Australia (Bookpurnong Formation) during the latest late Miocene to earliest Pliocene (Cheltenhamian) (section 4.3, section 4.4 and section 4.6).

However, during the mid early Pliocene (Kalimnan / mid Zanclean), there is a distinct east-west partition in *sorrenta*e-group distribution across the northern Bass Strait Seaway. *Neohornibrookella* (*sorrentae*-group) taxa occur in mid early Pliocene (Kalimnan) strata of the Jemmy's Point Formation (Gippsland Basin) near Lakes Entrance southeast Victoria (Kumbaric, 2013), a region adjacent to the eastern end of the modern day Bass Strait, and consequently strongly associated with East Australian Current waters. However, in coastal cliff exposures near Portland in southwest Victoria, adjacent to the western end of Bass Strait, the mid early Pliocene (Kalimnan) lower beds of the Whalers Bluff Formation (western Otway Basin) contain rich shallow normal marine ostracod faunas that lack *Neohornibrookella* spp. (Warne and Soutar, 2012). Similarly, in samples of the mid early Pliocene (Kalimnan) Grange Burn Formation near Hamilton southwest Victoria examined for this study (western Otway Basin), *Neohornibrookella* spp. are missing from otherwise rich shallow marine fossil ostracod faunas. The palaeogeographic position of this mid early Pliocene (Kalimnan) east-west partition in *Neohornibrookella* spp. distribution across southeast Australia appears to approximate Cape Otway in the western Bass Strait region (Fig. 1, Fig. 9 and Fig. 12B). This palaeobiogeographical partition is here referred to as the *Bassian Gateway*, and is likely to have been caused by a diminished influence of the East

Australian Current west of Cape Otway during the mid early Pliocene, and incursion of the Zeehan Current from the west (Fig. 12B). The hypothesis is supported by evidence of changed sedimentation patterns in submarine canyons of the western Bass Strait region, which suggest a change from predominantly westward flowing to eastward flowing currents during the Pliocene (Leach and Wallace 2001, Warne and Soutar, 2012). The advent of a strong eastward flowing surface current impinging on the western Bass Strait region during the Pliocene is here referred to as the *Zeehan Switch*. This palaeoceanographical event correlates with significant terrestrial palaeoclimatological change along the Nullarbor Plain of southern Australia (Sniderman *et al.*, 2016). During the late Miocene to Pleistocene there was significant narrowing of the Indonesian Seaway and consequent constriction of the Indonesian Throughflow (Srinivasan and Sinha, 1998), expansion of the Western Pacific Warm Pool (Li *et al.*, 2006), shifts in the intensity of surface currents associated with the North and South Pacific gyres (Srinivasan and Sinha, 1998; Wei, 1998), and inception (or substantial strengthening) of the Leeuwin Current (Gallagher *et al.*, 2009, 2014). All these palaeoceanographical events are likely to have had an impact on surface ocean currents around the southern Australian continental margin.

At the present day, the Zeehan Current, which runs southeastward along the continental shelf edge of western Bass Strait and western Tasmania is regarded as an extension of the Leeuwin current. While lacking *Neohornibrookella* species, the lower beds of the Whalers Bluff Formation near Portland contain some semi-thermophilic ostracod species (Warne and Soutar, 2012). These species perhaps reflect a Pliocene connection between the Zeehan Current and warm Leeuwin Current, as is apparent at the present day. Also of note, Quilty *et al.* (2013) have suggested some Pliocene north-south (latitudinal) variation in East Australian Current penetration into the eastern Bass Strait region.

The last strong signal of maritime warmth along the southern Australian continental margin occurs during the early late Pliocene (Piacenzian). This is evidenced by occurrences of the *Neohornibrookella* (*sorrentae*-group) Ostracoda in the Cameron Inlet Formation on Flinders Island in the eastern Bass Strait region of southeast Australia, and in the Roe Calcarenite from the southwest Australian coastal plain. These occurrences are probably a reflection of increased mid Pliocene, mid-high latitude global warming (e.g. Cronin *et al.,* 1993; Knies *et al.,* 2002). Significant mid Pliocene warming has been related to increased meridional oceanic heat transport associated with stronger thermohaline circulation, which enhanced sea ice retreat and caused a consequent decrease in high latitude albedo (Dowsett *et al.,* 1992; Raymo *et al.,* 1996). Further, Ravelo *et al.* (2004) and Wara *et al.* (2005) have suggested that permanent El-Niño-like meridional and zonal sea surface temperature gradients prevailed in the Pacific Ocean during the mid Pliocene. Given the lack of evidence for *Neohornibrookella* (*sorrentae*-group) taxa in the Pliocene or Pleistocene of the western Bass Strait region (section 4.2), early late Pliocene Cameron Inlet Formation *sorrentae*-group occurrences (far southeast Australia), and early late Pliocene Roe Calcarenite *sorrentae*-group occurrences (southwest Australia), are likely to be separately associated with palaeo-East Australian and Leeuwin currents respectively. The association of *sorrentae*-group Ostracoda with the Leeuwin Current, evident within the early late Pliocene Roe Calcarenite, may have origins in the migration of southwest Pacific *sorrentae*-group taxa into the northeast Indian Ocean via the Indonesian Throughflow. However, as we have not examined the Neogene marine strata of Western Australia in detail, the timing and pathway of migration of *Neohornibrookella* (*sorrentae*-group) taxa into southwest Australian shallow marine realms remains unestablished.

5.4. Ocean current impacts on coastal palaeoclimates of SE Australia

The increased biodiversity of *sorrentae*-group species in southeast Australia during the two periods, latest early to mid-Miocene (Batesfordian to Balcombian), and latest late Miocene (early Cheltenhamian), probably indicates periods of stronger East Australian Current influence around this region. Interestingly, Martin (1987, 1989, 1994, 2014) noted that while rainforest *Nothofagus* pollen decreased across inland southeast Australia during the early to mid Miocene, suggesting the prevalence of relatively dry climatic conditions, this pollen type persisted in high frequencies in coastal and extreme southeast Australian locations during the same time. Such a distribution of fossil *Nothofagus* pollen suggests a warm, humid climate in southeast Australian coastal regions, which is consistent with the nearby presence of strong warm plumes of East Australian Current waters. Similarly Martin (1994) and Kershaw *et al.* (1994) indicate a brief, but significant peak in *Nothofagus* pollen in terrestrial floral records across southeastern Australia ('Gymnosperm/*Nothofagus* phase') during the latest Miocene to earliest Pliocene. Again this closely matches an increase in biodiversity, and geographic distribution of *Neohornibrookella* species in shallow marine sediments of southeastern Australia, suggesting a link between warm, humid terrestrial climatic conditions, and pulses of warm East Australian Current waters.

Aside from these two brief intervals of increased *sorrentae*-group diversity and abundance, the persistent presence of this species group in southeastern Australia through the intervening middle to late Miocene period, as evidenced by records from the Nepean 1 borehole, implies a persistent coeval influence of East Australian Current waters across this region. This seems borne out by the persistence of *Nothofagus* pollen in the onshore Gippsland Basin in far southeast Australia during the late Miocene (Kershaw *et al.*, 1994). However, counteracting the warming effect of the East Australian Current in this region during this time, were intense episodes of late Miocene (Mitchellian) coastal upwelling (Li and McGowran, 1994; Warne,

2012). The cooling effect on coastal waters of late Miocene upwelling events, would have lessened the atmospheric warming and evaporative effects of warm East Australian Current waters. The interplay between warm East Australian Current and cold upwelling waters probably led to fluctuations in mid late Miocene (Mitchellian) climatic conditions across the southeast Australian coastal hinterland.

The occurrence of a *Neohornibrookella* (*sorrentae*-group) species in early late Pliocene (Piacenzian) strata on Flinders Island in the east of Bass Strait points to the presence of warm East Australia Current waters around southeastern Australia at this time. Warm early late Pliocene conditions in the eastern Bass Strait region were also recorded by Gallagher *et al.* (2003) based on Gippsland Basin foraminiferal and palynological proxy data. At the same time, along the northern Bass Strait hinterland, ostracod proxy data indicate high river discharges into coastal settings. From these ostracod data, Warne (2005) suggested that relatively wet (high rainfall) early late Pliocene climatic conditions prevailed across the southern Victorian coastal plain and adjacent inland ranges.

5.5 Disappearance of Neohornibrookella species from Bass Strait

Following the substantial late Miocene shallowing of the Bass Strait seabed during the Kosciusko Uplift in southeastern Australia (Warne, 2012), migrations of *Neohornibrookella* (*sorrentae*-group) species into the region were likely dependent upon strong westward flows of warm East Australian Current waters during periods of high eustatic sea level. The youngest known occurrences of *sorrentae*-group specimens in the Bass Strait region are within the early late Pliocene of the Cameron Inlet Formation on Flinders Island. The youngest normal marine strata along the northern Bass Strait hinterland examined for this study belong to the lower Werrikoo Limestone, this transgressive sequence having formed on the far west Victorian coastal plain during earliest Pleistocene (Gelasian / Werrikooian)

times. *Neohornibrookella* (*sorrentae*-group) taxa are absent from lower Werrikoo Limestone strata, perhaps because these lie west of Cape Otway, and thus formed under the influence of the southeastward flowing Zeehan Current rather than the East Australian Current (see discussion in section 5.3.2). *Neohornibrookella* (*sorrentae*-group) taxa have not been recorded in surveys of marine Ostracoda from modern-day Bass Strait (Yassini and Jones, 1995; Neil, 2000b), or adjacent coastal marine embayments (McKenzie, 1967), they therefore appear to have become extinct within this region at some time after the early late Pliocene.

Around the onset of the early Pleistocene (Gelasian) northern hemisphere glaciations, the southern hemisphere subtropical convergence is thought to have moved northwards shifting cool upwelling waters adjacent to the eastern Bass Strait continental shelf margin (Gallagher *et al.,* 2003) (Age framework reinterpreted on the basis of the International Commission on Stratigraphy review of Pliocene-Pleistocene boundary (Gibbard *et al.,* 2009)). This early Pleistocene cooling is likely to have intensified the Bass Cascade - a cold eastward-moving winter current operating in Bass Strait at least since this time (Mitchell *et al.,* 2007). At present, forcing by prevailing westerly winds (mid-latitude westerlies) produces this eastward-moving winter current, which is further propelled by relative cold dense and saline water in the east of Bass Strait sinking below the warmer, less saline water of the Tasman Sea (Godfrey *et al.,* 1980). It is possible that the inception or intensification of this cold winter current, post mid Pliocene global maritime warmth, accounts for the extinction of thermophilic *Neohornibrookella* (*sorrentae*-group) species within the Bass Strait region.

6. Conclusion

The genus *Neohornibrookella* Jellinek is here broadly defined on carapace morphology to include three species groups; the *transoceanica*-group, the *sorrentae*-group, and the *titanikos*-group. The Miocene distribution of *Neohornibrookella* species relates to surface ocean

currents associated with the North and South Pacific gyres. Mid Miocene species of the *sorrentae*-group in southeast Australia have carapace morphologies that suggest a heterochronic evolutionary relationship. In southeastern Australia, *sorrentae*-group ostracods first appear in the stratigraphical record in the late early Miocene, and seem strongly associated with East Australian Current waters. The distribution of this species group has been used to define a new marine palaeobiogeographical transition zone, the Bassian Gateway, which relates to the early Pliocene inception, or strengthening, of the Zeehan Current in the west of the Bass Strait seaway.

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Appendix. Systematic taxonomy

1.1 Higher Classification

Phylum Crustacea Pennant, 1777

Class Ostracoda Latreille, 1806

Order Podocopida Müller, 1894

Suborder Podocopina Sars, 1866

Superfamily Cytheroidea Baird, 1850

Family Thaerocytheridae Hazel, 1967

Subfamily *Tenedocytherinae* nov.

1.1.1 Diagnosis

The Tenedocytherinae includes thaerocytherid genera with medium to large adult carapaces and course reticulate ornament. Some muri are developed into posterodorsal ridges. Carapace characterised by a subcentral tubercle of varying strength, which internally includes four adductor muscle scars plus two or three frontal scars (e.g. Fig. 8). The upper frontal scar is never divided. The lower frontal scar is sometimes subdivided, partially or fully, into two scars. Other internal features typical for the Thaerocytheridae. Included genera are

Tenedocythere Sissingh, 1972, *Bosasella* Bonaduce, 1985 and *Neohornibrookella* Jellinek, 1993. These three genera display a disjunct bimodality in carapace ontogenetic development with adult and A-1 specimens usually being subrectangular in lateral view, and early instars being subtriangular in lateral view (e.g. Fig. 6).

1.1.2 Remarks

Early stage juveniles of all tenedocytherine species possess a triangular carapace in outline and usually a very prominent posterodorsal spine (Fig. 7). This posterodorsal spine is larger in early stage juveniles relative to carapace size, than in adult specimens. The similar disjunct bimodal patterns of ontogenetic development in species of *Neohornibrookella, Tenedocythere* and *Bosasella,* coupled with the similar early stage instar carapace morphology for all species of these genera (e.g. Fig 7 (this study) and Bonaduce *et al.,* 1986, text-figs 4, 5), are here considered to likely reflect close phylogenetic relationships between these genera. All known species of the Tenedocytherinae lack the truncated left valve posterodorsal margin of thaerocytherid species belonging to the Bradleyinae Benson, 1972. The Tenedocytherinae have an essentially Paratethyan (Mediterranean) and equatorial west Pacific geographic distribution, but have spread from the west Pacific Ocean, via equatorial currents, into the Indian Ocean, as well as the Caribbean Sea and adjacent coastal regions. The evolutionary origins of the Tenedocytherinae likely extend back to divergence from Palaeogene thaerocytherines belonging or allied to the genus *Hornibrookella* Moos, 1965. The currently known stratigraphical range of the Tenedocytherinae is Miocene to Recent.

1.2 Genus Neohornibrookella Jellinek, 1993

1.2.1 Type species

Cythere lactea Brady, 1866 (*sensu* Jellinek, 1993)

1.2.2 Emended Diagnosis

A subrectangular tenedocytherine genus distinguished by an oblique alignment of fossae, the muri of which are usually thickened to form obliquely aligned ridges, extending from the subcentral tubercle to the posterodorsal cardinal angle, typically terminating in a small spine or node. Posterodorsal ridges do not form part of a posterodorsal loop (*sensu* Benson, 1972; fig.9). Posterodorsal hinge-ear ridge (*sensu* Bonaduce *et al.*, 1986, text fig. 2) subdued or absent.

1.2.3 Remarks

The concept of *Neohornibrookella* adopted here is based on the valve and carapace specimens from Kenyan coastal waters used by Jellinek (1993) to define this genus and identified by this author as belonging to the species *Cythere lactea* Brady, 1866. This is a misidentification; these Kenyan species in fact belonging to *Neohornibrookella transoceanica* Teeter, 1975. Resolution of this issue is beyond the scope of the current work and will be dealt with by the present authors in a subsequent paper.

1.3. Neohornibrookella sorrentae **(**Chapman and Crespin, 1928)

Figs 2A–F; 3A–F; 4A–F; 7A–F; 8A–C

1914 *Cythere lactea* Brady; Chapman, p.36; pl.7, fig. 15.

1916 *Cythere lactea* Brady; Chapman, pl.73, fig. 15.

1928 *Cythere lactea* Brady; Chapman and Crespin, p.124–125.

1928 *Cythere sorrentae* sp. nov. Chapman and Crespin, p. 124, pl. 9, fig. 63a, b.

1981 *Tenedocythere* [non *lactea*?], McKenzie, p.106.

1981 *Tenedocythere* [?] [juv.], McKenzie, p.107.

1987 *Hermanites* sp. 1 Warne (pars), p. 442.

1994 *Hermanites glyphica* sp. nov. Neil (pars), pl. 7, figs 4, 5.

2000a *Hermanites glyphica* Neil; Neil (pars), pl. 1, fig. 2.

2006 *Hermanites glyphica* Neil, p. 51, fig. 5C–E.

1.3.1. Holotype.

The holotype specimen of *N. sorrentae* (NMV P14431) designated by Chapman and Crespin (1928) is an early stage juvenile left valve (Fig. 7A). One significant characteristic of this specimen is its extremely faint reticulate ornament. The type locality for *N. sorrentae* is within the Nepean 1 borehole at 331.6 m (see details in appendix section *1.3.2*). For this study eighteen samples between 438.9 m to 303.3 m in Nepean 1 borehole, each approximately 20 – 50 grams of washed > 65µ residue, were examined for *N. sorrentae* specimens. Early stage *N. sorrentae* juvenile specimens were found to be common in these samples, all of which possess very weak or no reticulate ornament, similar to the juvenile *N. sorrentae* holotype specimen. This interval within the Nepean 1 borehole is mostly a clayey silt of middle Miocene to early late Miocene age (Bairnsdalian; Fig. 11). Throughout this Nepean 1 interval, all adult specimens of *N. sorrentae* belong to *morphotype 1* as here defined (Fig. 2A, B). Thus, all thirty-four *N. sorrenta*e juvenile specimens (including the holotype), together with the nine adult specimens collected from the interval 439.9 m to 303.3 m appear to belong to *morphotype 1* of this species.

Compared to early stage juveniles of *N. sorrentae* (*morphotype 1*), similar sized juvenile specimens of *N. sorrentae* (*morphotype 2*) (Fig. 7E) possess a more expansive coverage of

reticulate ornament in the posterior half of valves. This is likely to be ecophenotypic variation.

Compared to early stage juveniles of *N. sorrentae* (all morphotypes), similar sized juvenile specimens of *N. nepeani* sp. nov. (Fig. 6F) possess consistently and conspicuously stronger reticulate ornament over both the anterior and posterior surface of valves. This is interpreted as a species level difference in juvenile carapace morphology. Compared to early stage juveniles of *N. sorrentae* (all morphotypes), similar sized juvenile specimens of *N. glyphica* (Fig. 7G-H) possess more elongated valves, with a greater length to height ratio. In addition, early stage juvenile specimens of *N. glyphica* have a less strongly tapered posterior than early stage juvenile specimens of *N. sorrentae* or *N. nepeani*. The slight differences in early instar lateral outline between these species are evident despite the presence of minor precocious sexual dimorphism in early instar valve shape for these species.

Thus while the holotype specimen of *N. sorrentae,* being an early stage instar, lacks important species level diagnostic features, we argued above that this holotype specimen is likely to form part of the ontogenetic series of a *N. sorrentae* (*morphotype 1*) individual. As a consequence the identity of adult specimens for this species is not here considered in doubt. The requirement for the designation of a Neotype according to Article 75.3 of the International Code of Zoological Nomenclature (4th Edition) (ICZN, 1999) is that there "is an exceptional need" in order to clarify the taxonomic status of a nominal species. With respect to *N. sorrentae,* we do not consider that the ICZN "exceptional need" condition is yet met, and as a consequence no Neotype is designated.

1.3.2 Type locality and horizon

Nepean 1 borehole near Sorrento, Victoria (Lat. 38.33644° S; Long. 144.73812° E) at 331.6m (1088'). Fyansford Formation, Late Miocene (late Bairnsdalian).

1.3.3. Material studied

Forty-eight adult and juvenile specimens from the Fyansford Formation in the Nepean 1 borehole near Sorrento, Victoria, between the depths of 259.1 metres and 438.9 metres, (Port Phillip Basin). Forty one adult and juvenile specimens from the Batesford Limestone and Fyansford Formation in the Batesford Cement Quarry ("new" Batesford Quarry, Port Phillip Basin). Eleven specimens from the Flinders Limestone in coastal cliffs near Flinders (Western Port Basin).

1.3.4 Dimensions

Morphotype 1: P143645, LV adult female, L=1.07mm, H=0.63mm; P143646, RV adult female, L=1.06mm, H=0.62mm; P143647, LV adult male, L=1.07mm, H=0.61mm.

Morphotype 2: P143648, LV adult male, L=1.06mm, H=0.62mm; P12509, RV adult female, L=1.06, H=0.58mm.

Morphotype 3: P143650, RV adult female, L=1.03mm, H=0.60mm; P143651, LV adult female, L=1.00mm, H=0.60mm; P143652, RV adult male, L=1.01mm, H=0.58mm.

1.3.5 Emended Diagnosis

A relatively large thaerocytherid species with weak oblique ridges and / or lines of fossae extending from subdued subcentral tubercle to the posterodorsal region of the carapace terminating as a small but distinct spine or node that extends beyond the dorsal margin. Externally the subcentral tubercle is traversed by a small oblique rib.

1.3.6 Additional description

A large, thick shelled species with subrectangular to subtriangular shaped adult and A-1 juvenile valves in lateral view (Fig. 2A-F; Fig. 3A-D; Fig. 4A-F). A more markedly triangular lateral view shape is apparent in early stage juveniles (Fig. 7A, D, E). The shift from a strongly triangular lateral view shape in early stage juveniles to a generally more subrectangular lateral view shape in adults gives rise to a distinct (disjunct) bimodality in ontogenetic shape development. In adults anterior margin broadly and evenly rounded; dorsal margin straight (in *morphotype 1*) to concave (in *morphotypes 2* and *3*); ventral margin straight to slightly concave; posterodorsal margin concave; posteroventral margin developed as a short although prominent caudal process. The caudal process is also prominent in early stage juvenile valves. More or less equivalved, although RV very slightly larger than LV. Maximum length below mid-height; maximum height anterior of mid-length (at anterodorsal cardinal angle). In dorsal view, carapace widest at the subcentral tubercle and terminal spine of the ventral ridge (Fig. 4E). The anterior and posteroventral margins of adult valves (and to a lesser extent juvenile valves) carry numerous short spines, which are commonly abraded. The largest of these marginal spines occurs at the posterodorsal cardinal angle (Fig. 2C). Adult and juvenile valves possess a strongly alate ventral ridge that terminates posteriorly in a blunt spine or node (e.g. Fig. 2A and Fig. 4F). In adults and A-1 juveniles, a strong submarginal ridge runs parallel to the anterior margin extending from a distinct eye tubercle to the anteroventral margin. This anterior ridge is separated from the anterior margin by an arc of 7 or 8 large fossae (Fig. 2A-C, E, F; Fig. 3A, C, D; Fig. 4B-D, F). These fossae, although not the submarginal ridge, are apparent adjacent to the anterior margin of early stage juvenile valves (Fig. 7A, D, E). Strong reticulate ornament occurs across the external surface of adult and A-1 juvenile valves, the muri of which may develop into weak ridges in the dorsal and posterodorsal regions of the carapace (e.g. Fig. 3A and Fig. 4B). These ridges terminate posteriorly as a prominent short posterodorsal spine or node that generally extends

beyond the dorsal margin in lateral view, and which is positioned immediately anterior of a sometimes also prominent posterodorsal marginal spine. Reticulation is much weaker in early stage juvenile specimens, and where present, more prominent in the posterior than anterior half of the carapace (Fig. 7A, D, E). Early stage juveniles do not possess the dorsal and posterodorsal ridges of some adults, but always strongly express the associated terminal spine (Fig. 7A, D, E). Eye tubercle present. A very short, but distinct rib generally overlies an indistinct subcentral tubercle. Heavy holoamphidont hinge with crenulated medium element. Inner lamella moderately broad. Within the interior of valves, numerous large normal pore canals are obvious. Central muscle scars located within interior depression associated with subcentral tubercle. Adductor scars somewhat obscured, but appear to consist of an oblique row of four elongate scars, the uppermost generally divided. Frontal scars consisting of 2 to 3 individual scars. The uppermost frontal scar is irregularly rounded (sometimes heart shaped; Fig. 7B). The lower frontal scar is generally divided into discrete, but abutting scars (Fig. 7B). (NB. The frontal muscle scar pattern can vary in appearance, especially with respect to scar subdivision, depending on the method of viewing. For instance compare SEM image and transmitted light microscope image of muscle scar region of same specimen in Fig. 7B and Fig. 7C).

1.3.7 Remarks

The three morphotypes for this species defined in section 5.2, slightly vary in size, shape and ornament. These can be summarised as follows. Specimens from the deeper end of this species' palaeoecological range (middle shelf) do not have muri differentially thickened as surface ridges (= *morphotype 1*). Specimens from the shallowest end of this species palaeoecological range (inner shelf) are smaller, and have selected muri differentially thickened as surface ridges (= *morphotypes 3*). Morphological intermediaries (*morphotype 2*)

occupied intermediate depth ranges between that of *morphotypes 1* and *3* (Fig. 10). Sexual dimorphism is the same for all morphs. In adult males there is a slightly greater difference between the carapace heights at the anterior and posterior cardinal angles than in adult females. Male valves thus have a somewhat more tampered posterior and elongated appearance in lateral view than female valves. The age range of this species in southeastern Australia is from early Miocene to late Pliocene.

1.4. Neohornibrookella glyphica **(**Neil, 1994)

Figs 5A-F; 7G-I, N-O; 8E-F

1987 *Hermanites* sp. 1 Warne (pars), p. 442.

1994 *Hermanites glyphica* sp. nov. Neil (pars), p. 17, pl. 7, fig. 3.

2000a *Hermanites glyphica* Neil; Neil (pars), pl. 1, fig. 1, 3.

1.4.1 Holotype

Holotype, P123249, LV adult.

1.4.2 Type locality and horizon

Bank of Grange Burn, opposite Henty's House, near Hamilton (Lat. 37.72366° S; Long. 141.9425° E). Muddy Creek Marl, early mid-Miocene.

1.4.3 Materials studied

Twelve adult and juvenile specimens from the Batesford Limestone and Fyansford Formation in the Batesford Cement Quarry ("new" Batesford Quarry, Port Phillip Basin). Forty eight specimens from the Flinders Limestone in coastal cliffs near Flinders (Western Port Basin).

Six adult and juvenile specimens from the Warneet Sands in the Sherwood 18 borehole from 20 to 22 metres depth.

1.4.4 Dimensions

P143655, LV adult male, L=0.98mm, H=0.56mm; P143656, LV adult female? (slightly damaged), L=0.96mm, H=0.58mm; P143657, LV adult female, L=0.97mm, H=0.58mm; P122640, RV adult female, L=0.94mm, H=0.55mm.

1.4.5 Emended diagnosis

A moderate to large species of *Neohornibrookella* with a strong subcentral tubercle, and strong, but blunt posterodorsal spine. A short ridge occurs at mid height in the posterior half of the carapace.

1.4.6 Additional description

A moderately large, thick shelled species with subrectangular shaped adult and A-1 juvenile valves in lateral view (Fig. 5A-F). A triangular lateral view outline is apparent in early stage juveniles (Fig. 7G-I). In adults anterior margin broadly and evenly rounded; dorsal margin more or less straight; posterodorsal margin marked by a strong blunt spine; posteroventral margin has a distinct caudal process in RV, which is less obvious in LV. RV very slightly larger than LV. Maximum length below mid height; maximum height anterior of mid length (at anterodorsal cardinal angle). In dorsal view, carapace widest at the subcentral tubercle and posterior termination of the ventral ridge. The posteroventral margins of adult valves carry a few short spines, although in most specimens examined for this study, these have been worn away. Adult and juvenile valves possess a strongly alate ventral ridge, which is thickened at its posterior termination, sometime resembling a blunt node (e.g. Fig. 5A and Fig. 4F). In adults and A-1 juveniles a strong submarginal ridge extends parallel to the

anterior margin from a distinct eye tubercle to the anteroventral margin. This anterior ridge is separated from the anterior margin by an arc of 7 or 8 large fossae (Fig. 5A-C). These fossae, but not the submarginal ridge, are apparent adjacent to the anterior margin of early stage juvenile valves (Fig. 7G-I). Strong reticulate ornament occurs across the external surface of adult and A-1 juvenile valves. Some muri are developed into ridges in the dorsal, posterodorsal and posterior regions of the carapace (e.g. Fig. 5A-F). Particularly characteristic of this taxon, amongst the *sorrentae* species group, is the presence of a short medium ridge immediately posterior of the subcentral tubercle. Two weak ridges are developed in the dorsal region on the carapace, one of which terminates posteriorly as a strong, blunt posterodorsal spine or node that extends beyond the dorsal margin in lateral view. The ventral ridge forms an alate extension adjacent to the ventral margin. Eye tubercle present. Inner lamella moderately broad. Heavy holoamphidont hinge. Muscle scars consisting of an oblique row of four adductor scars with two frontal scars (see also Neil, 1994).

1.4.7 Remarks

Of the range of specimens illustrated for *Hermanites glyphica* by Neil (1994), only the holotype specimen is here considered to definitely belong to this species. As with *Neohornibrookella sorrentae,* a number of morphotypes (two) of *Neohornibrookella glyphica* are present in Neogene marine sediments in southeastern Australia. These morphotypes mostly vary in posterodorsal ornament of left valve specimens (Figs 5A, C and 8E = *morphotype 1*; Figs 5D and 8F = *morphotype 2*). Both morphotypes occur in carbonate sand facies, but morphotype 2 appears to predominate in quartz sand facies. The holotype of *N. glyphica* illustrated by Neil (1994; plate 7, fig. 3) is a *morphotype 2* specimen. Sexual dimorphism subtle, with adult male valves having a slightly greater length to height ratio

compared to adult female valves. The age range of this species in southeastern Australia is latest early Miocene to early mid-Miocene, and latest late Miocene.

1.5. Neohornibrookella nepeani sp. nov.

Figs. 6A-F; 7F, P-Q; 8D

1.5.1 Derivation of name

With reference to the type locality being situated on the Nepean Peninsula, Victoria, Australia.

1.5.2 Holotype and Paratype

Holotype, P305748, LV adult male; Paratype P305749, RV adult male.

1.5.3 Type location and horizon

Nepean 1 borehole (Lat. 38.33644° S; Long. 144.73812° E) at the depth 178.3m. (Sediment sample material from this Nepean 1 core interval is available within the "stratigraphic collections" of Museum Victoria.)

1.5.4 Materials studied

Seven adult and juvenile specimens from the Nepean 1 borehole at 178.3m.

1.5.5 Dimensions

Holotype, P305748, LV adult male, L=1.10mm, H=0.62mm; Paratype, P305749, RV adult male, L=1.11mm, H=0.61mm.

1.5.6 Diagnosis

A large species of *Neohornibrookella* with strong ridge ornament developed in the ventral, dorsal and posterior of the carapace, which includes a diagnostic short sinuous, swirl-like, ridge that partially wraps around several fossae in the posterodorsal region of the carapace (Fig. 7P-Q; Fig. 8D).

1.5.7 Description

A large, thick-shelled species with subrectangular to subtriangular shaped adult and A-1 juvenile valves in lateral view (Fig. 6A-D). A triangular lateral view shape is apparent in early stage juveniles (Figs 6F; 7F). In adults anterior margin broadly and evenly rounded; dorsal margin concave; ventral margin more or less straight; posterodorsal margin concave; posteroventral margin developed as a short caudal process. RV slightly larger than LV. Maximum length below mid height; maximum height anterior of mid length (at anterodorsal cardinal angle). Carapace widest at the subcentral tubercle and terminal node on the ventral ridge. The posteroventral margins of adult and juvenile valves carry six short spines, when not abraded. Adult and juvenile valves possess a strongly alate ventral ridge that terminates posteriorly in a blunt spine or node. In adults and late stage juveniles a strong submarginal ridge runs parallel to the anterior margin extending from a distinct eye tubercle to the anteroventral margin. This anterior ridge is separated from the anterior margin by an arc of 7 or 8 large fossae (Fig. 6A-B). This curved line of fossae is apparent adjacent to the anterior margin of early stage juvenile valves (Fig. 6E; Fig.7F). Strong reticulate ornament occurs across the external surface of adult and juvenile valves, even on early stage instars. Various muri of the reticulum are thickened to form ridges in the dorsal and posterodorsal regions of the carapace (e.g. Fig. 6A-B, E). For the most part these ridges are linear, except in the posterodorsal region of the carapace, where one ridge wraps around several fossae, giving this particular ridge a sinuous appearance (Figs 7P-Q; 8D). In lateral view several of the

short posterodorsal ridges coalesce to form a blunt spine or node that slightly extends beyond the dorsal margin (in lateral view) in both adults and late stage juveniles, but more so in early stage juveniles. Subcentral tubercle prominent, externally on which is superimposed, a short oblique rib. In early stage juvenile specimens that lack well developed lateral surface ridges, the fossae of the reticulation form a broadly circular pattern around the subcentral tubercle. Heavy amphidont hinge. Inner lamella moderately wide. Within the interior of valves, numerous large normal pore canals are obvious. Central muscle scars located within interior depression associated with subcentral tubercle. Adductor scars and frontal scars somewhat obscure in the specimens studied, but appear consistent for the genus.

1.5.8 Remarks

The pattern of ridges in the posterodorsal region of *Neohornibrookella nepeani*, which includes one short sinuous ridge wrapped around several fossae, is so far unique to this taxon within the *sorrentae*-group of species. Sexual dimorphism unclear because of the limited number of adult specimens. However, comparison between available adult and juvenile specimens indicates that male valves are probably more elongate than female valves. This species is currently only known from the latest late Miocene of southeastern Australia.

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Figure captions

Figure 1. Locality diagram for *sorrentae*-group occurrences in Australia recorded in this study (sections 4.1-4.7). Geographic coordinates indicated in section 4. Solid circle are Miocene occurrences, open circles are Pliocene occurrences. Port Phillip Basin locations: 1. Batesford Limestone Quarry, near Geelong; 2. embankment behind Western Beach, Geelong; 3. mouth of Gunyoung Creek near Mornington; 4. Nepean 1 borehole near Sorrento; 5. coastal cliffs near Beaumaris (suburb of Melbourne); 6. hillside on east side of the Moorabool River under the railway viaduct on Geelong-Ballarat rail line. Western Port Basin locations: 7. coastal bluff at the Back Beach near Flinders; 8. Sherwood 18 borehole near Warneet; 9. Tyabb 1, 22 & 40 boreholes near Tyabb; 10. Koo-wee-rup 14 borehole near Koo-wee-rup; 11. French Island 7 & 8002 boreholes from the western coastal region of French Island. Gippsland Basin locations: 12. Brock's Quarry near Longford; 13. "Skinners" on the northern side of the Mitchell River valley, near Lindenow; 14. Lakes Entrance Oil Shaft at Lakes Entrance; 15. "Driers" on the north side of the Mitchell River valley, near Bairnsdale; 16. Moondarra Farm (near "Rose Hill") adjacent to the right bank of the Mitchell River west of Bairnsdale; 17. end of Ferndale Parade, Lakes Entrance; 18. road cut on the Princess Highway adjacent to Bunga Creek, near Lake Entrance. Bass Basin location: 19. between Lackrana and Memana on Flinders Island (Tasmania) in Bass Strait. Otway Basin Locations: 20. Yellow Bluff on Zeally Bay near Torquay; 21. north bank of Grange Burn (creek), opposite Henty's House, near Hamilton; 22. outcrop along the northwestern shore of Lake Bullen Merri, Camperdown. Murray Basin locations: 23. Murray River cliffs south of Morgan, South Australia; 24. Mallee Bore 11 near Murrayville; 25. Loxton Drainage Shaft No. 18 near Loxton, South Australia. Eucla Basin location: 26. shallow quarry between Madura and Eucla, Western Australia.

Figure 2. *Neohornibrookella sorrentae* (Chapman and Crespin, 1928), [*morphotype 1*]. Deepest water morphotype from mid-late Miocene mid-shelf mudstones. All images x 71. **A,** LV, A-1 juvenile female, external view, P143643, x71. **B,** RV, A-1 juvenile male?, external view, P143644. **C,** LV, adult female, external view, P143645. **D,** RV adult female, internal view, P143646. **E,** LV adult male, external view, P143647. **F,** RV adult female, external view, P143646. Locality details: All specimens from Nepean 1 borehole; **A–B, F,** from 387.0 m (middle Miocene); **C–D,** from 285.9 m (late Miocene); **E,** from 210.3 m (late Miocene). Scale bar = 0.5mm.

Figure 3. *Neohornibrookella sorrentae* (Chapman and Crespin, 1928), [*morphotype 2*]. Intermediate depth morphotype from mid Miocene inner-shelf marls and calcareous sands. All images x 71. **A,** LV adult male, external view, P143648. **B,** RV adult female, internal view, P12509. **C,** LV A-1 juvenile male, external view, P143649. **D,** RV adult female external view, P12509. [Images **B & D** are of a specimen misidentified by Chapman, 1914 & 1916 as *Cythere lactea* Brady, 1866]. Details of locations: **A & C,** from Fyansford Formation below upper limit of *Lepidocyclina* sp. in the Batesford Limestone Quarry near Geelong, Victoria (early Miocene); **B & D,** from the Mallee Bore N$^{o.}$ 11 between 171.3m and 171.9m. Scale bar = 0.5mm.

Figure 4. *Neohornibrookella sorrentae* (Chapman and Crespin, 1928), [*morphotype 3*]. Shallowest water morphotype from mid Miocene inner shelf marls and calcarenites. All images x 71. **A,** RV adult female, internal view, P143650. **B,** RV adult female, external view, P143650. **C,** LV adult female, external view, P143651. **D,** RV adult male, external view, P143652. **E,** carapace, dorsal view, P143653. **F,** RV A-1 juvenile?, female, external view, P143654. Details of locations: **A, B, D-F,** from Fyansford Formation below upper limit of *Lepidocyclina* sp. in the Batesford Limestone Quarry near Geelong, Victoria (early

Miocene); **C,** from Batesford Limestone (main *Lepidocyclina* horizon) in Batesford Limestone Quarry (early Miocene). Scale bar = 0.5mm.

Figure 5. *Neohornibrookella glyphica* (Neil, 1994). From latest early Miocene to early middle Miocene, and latest Late Miocene inner shelf calcarenites and calcareous sands. All images x 71. **A,** LV adult male, external view, P143655. **B,** LV adult female?, external view, P143656. **C,** LV adult female, external view, P143657. **D,** RV adult female, external view, P122640. **E,** LV A-1 juvenile female, external view, P305746. **F,** RV A-1 juvenile male, external view, P305747. Details of locations: **A, E & F,** from Flinders Limestone (*Lepidocyclina* horizon) exposed in coastal cliffs near Flinders, Victoria (early Miocene); **B & C,** from Batesford Limestone (main *Lepidocyclina* horizon) in Batesford Limestone Quarry, near Geelong, Victoria (early Miocene); **D,** from Warneet Sands in the Sherwood 18 borehole near Warneet, Victoria from 20-22 metres (latest Miocene). Scale bar = 0.5mm.

Figure 6. *Neohornibrookella nepeani* sp. nov. From latest late Miocene inner shelf calcareous sands. All images x71. **A,** Holotype, LV adult male, external view, P305748. **B,** Paratype, RV adult male, external view, P305749. **C,** Paratype, RV adult male, internal view, P305749. **D,** Holotype, LV adult male, internal view, P305748. **E,** LV late stage juvenile female?, external view, P305750. **F,** LV early stage juvenile, external view, P305751. All illustrated specimens from basal nodule bed of Black Rock Sandstone (Sandringham Sands) in the Nepean 1 borehole near Sorrento, Victoria at 178.3m. Scale bar = 0.5mm.

Figure 7. **A,** *Neohornibrookella sorrentae* (Chapman and Crespin, 1928), [*morphotype 1*], Holotype, LV, early stage juvenile, external view, P14431, x 71. **B,** *N. sorrentae*, [*morphotype 3*], RV adult female, internal view of frontal and adductor muscle scars imaged with SEM, P143650, x 268. **C,** *N. sorrentae*, [*morphotype 3*], RV adult female, internal view of frontal and adductor muscle scars imaged with under transmitted light microscope,

P143650, x 268. **D,** *N. sorrentae,* [*morphotype 1*], LV early stage juvenile, external view, P305752, x 71. **E,** *N. sorrentae*, [*morphotype 2*], LV early stage juvenile, external view, P314962, x 71. **F,** *Neohornibrookella nepeani* sp. nov., LV early stage juvenile, external view, P314963, x 71. **G,** *Neohornibrookella glyphica* (Neil, 1994), LV early stage juvenile, external view, P314964., x71 **H,** *N. glyphica*, LV early stage juvenile, external view, P314965, x 71. **I,** *N. glyphica*, RV early stage juvenile, external view, P314966, x 71. **J,** *N. sorrentae*, [*morphotype 1*], LV A-1 juvenile male, view of exterior posterodorsal ornament, P143647, x 71. **K,** *N. sorrentae,* [*morphotype 1*], LV A-1 juvenile female, view of exterior posterodorsal ornament, P143643, x 71. **L,** *N. sorrentae,* [*morphotype 2*], LV adult male, view of exterior posterodorsal ornament, P143648, x 71. **M,** *N. sorrentae,* [*morphotype 3*], LV adult female, view of exterior posterodorsal ornament, P143651, x 71. **N,** *N. glyphica* (Neil, 1994), LV adult male, view of exterior posterodorsal ornament, P143655, x 71. **O,** *N. glyphica,* LV adult female, view of exterior posterodorsal ornament, P143657, x 71. **P,** *N. nepeani*, LV adult male, view of exterior posterodorsal ornament, P305748, x 71. **Q,** *N. nepeani*, RV adult male, view of exterior posterodorsal ornament, P305749, x 71. **R,** *N. sorrentae,* [*morphotype 1*], LV A-1 juvenile male, external view, arrow points to subdued sinuosity of dorsal margin posterior of anterodorsal cardinal angle, P143647, x 84. **S,** *N. sorrentae* [*morphotype 2*]. LV A-1 juvenile male, external view, arrow points to marked sinuosity of dorsal margin posterior of anterodorsal cardinal angle, P143649, x 83. Details of locations: *N. sorrentae* [*morphotype 1*]; **A,** from Fyansford Formation in Nepean 1 borehole near Sorrento, Victoria at 331m (mid-late Miocene); **D, J, R,** from Fyansford Formation in Nepean 1 borehole at 210.3m (late Miocene); **K,** from Fyansford Formation in Nepean 1 borehole at 387.0m (middle Miocene). *N. sorrentae* [*morphotype 2*]; **E, L, S,** from Fyansford Formation (*Lepidocyclina* horizon) in the Batesford Cement Quarry near Geelong, Victoria (early Miocene). *N. sorrentae* [morphotype 3]; **B. C, M,** from Fyansford Formation

(*Lepidocyclina* horizon) in Batesford Limestone Quarry (early Miocene). *N. glyphica*; **G-I, N,** from the Flinders Limestone (*Lepidocyclina* horizon) in coastal cliffs near Flinders, Victoria (early Miocene); **O.** from the Batesford Limestone (*Lepidocyclina* horizon) in the Batesford Cement Quarry (early Miocene). *N. nepeani*; **F, P, Q,** from the Back Rock Sandstone (Sandringham Sands) in the Nepean 1 borehole at 178.3m (late Miocene).

Figure 8. Maps of external fossae and ridges in posterodorsal region of left valves. **A,** *Neohornibrookella sorrentae* (Chapman and Crespin, 1928), [*morphotype 1*], A-1 juvenile female, P143643, x 63. **B,** *N. sorrentae*, [*morphotype 2*], adult male, P143648, x 64. **C,** *N. sorrentae*, [*morphotype 3*], adult female, P143651, x 65. **D,** *Neohornibrookella nepeani* sp. nov., adult male, P305748, x 61. **E,** *Neohornibrookella glyphica* (Neil, 1994), adult female, P143657, x 71. **F,** *N. glyphica*, adult female, P122639, x 68. Details of locations: **A,** from Fyansford Formation in Nepean 1 borehole near Sorrento, Victoria at 387.0m; (middle Miocene) **B,** from Fyansford Formation (*Lepidocyclina* horizon) in Batesford Cement Quarry near Geelong, Victoria (early Miocene); **C, E,** from Batesford Limestone (main *Lepidocyclina horizon*) in Batesford Cement Quarry (early Miocene); **D,** from basal nodule bed of Black Rock Sandstone (Sandringham Sands) in the Nepean 1 borehole at 178.3m (late Miocene); **F,** from Warneet Sands in Sherwood 18 borehole near Warneet, Victoria from 20-22 metres.

Figure 9. Biogeographical and palaeobiogeographical distributions of *Neohornibrookella* species groups. Open symbols are of representative fossil occurrences; solid symbols are of representative modern occurrences. Note, very limited data available with respect to fossil occurrences in southwest and northern Australia, and for the island of New Guinea. Distributions interpreted from data presented in section 4, and previous studies by Teeter (1975), Holden (1976), Bonaduce *et al.*(1980), Hartmann (1981), Jellinek (1993) and

Coimbra and Carreño (2012), Whatley and Jones (1999), Whatley *et al.* (2000, 2004) and Titterton and Whatley (2008). Palaeobiogeographical Gateways: 1. Tethyan Ocean Gateway; 2. Indonesian Throughflow; 3. Bassian Gateway; 4. Isthmus of Panama.

Figure 10. Lithological and palaeoenvironmental ranges of *Neohornibrookella* species in Neogene strata of the Port Phillip and Western Port basins, SE Australia. Solid line = autochthonous occurrences; dashed lines = allochthonous or uncertain occurrences. Palaeoenvironmental ranges interpreted from data presented in sections 5.2.1–5.2.3.

Figure 11. Chronostratigraphical ranges of *Neohornibrookella* (*sorrentae*-group) species in Port Phillip and Western Port basins (PP & WP) (4th column form left), and taxonomically broad *sorrentae*-group records for southeastern Australia (5th column from left). Temporal distribution of ostracod taxa determined by matching against planktonic foraminifera occurrences recorded by Mallett (1977), Mallett and Holdgate (1985), McGowran and Li (1993) and Li and McGowran (2000), and by matching with molluscan based stratigraphical correlations in Darragh (1985). SE Australian stage boundaries defined as follows: Base of Longfordian defined by the First Appearance Datum (FAD) of the planktic foraminiferan *G. dehiscens*. Longfordian–Batesfordian boundary is characterised by an abundance of the warm water benthic foraminiferan *Lepidocyclina howchini* in shallow marine carbonate facies in the Port Phillip Basin. The FAD of *P. sicanus* is taken as the Longfordian–Batesfordian boundary. Batesfordian – Balcombian boundary marked by the disappearance of *Lepidocyclina howchini* in the Port Phillip Basin. This occurs between the FAD's of *P. sicanus* and *P. glomerosa.* The Balcombian–Bairnsdalian boundary occurs after the FAD of *O. suturalis* around the FAD of *P. mayeri.* The Bairnsdalian–Mitchellian is ill-defined but occurs in the time range between the FAD's of *N. acostaensis* and *G. conomiozea*. The Mitchellian–Cheltenhamian boundary occurs between the FAD's of *G. conomiozea* and *G.*

crassaformis. The Cheltenhamian–Kalimnan boundary approximates the FAD of *G. punticulata* and the top of the Kalimnan stage occurs well prior to the FAD of *G. truncatulinoides.* The FAD of *N. acostaensis* is taken as the middle–late Miocene boundary, and the FAD of *G. crassaformis* approximates the Miocene–Pliocene boundary. For further discussion on the relationships between planktonic foraminiferal datums and Australian Neogene geological stages see Mallett and Holdgate, (1985), Abele *et al.* (1988), Carter (1990), Li and McGowran (2000) and Warne and Soutar (2012).

Figure 12. Schematic diagram of major surface ocean currents during (A) the latest Early Miocene (Batesfordian), and (B) the mid early Pliocene (Kalimnan). PWP – Pacific Warm Pool, EAC – East Australian Current, TF – Tasman Front, LC – Leeuwin Current, ZC – Zeehan Current; EGC – Eastern Gyral Current; WAC – West Australian Current, ACC – Antarctic Circumpolar Current.

Fig. 1

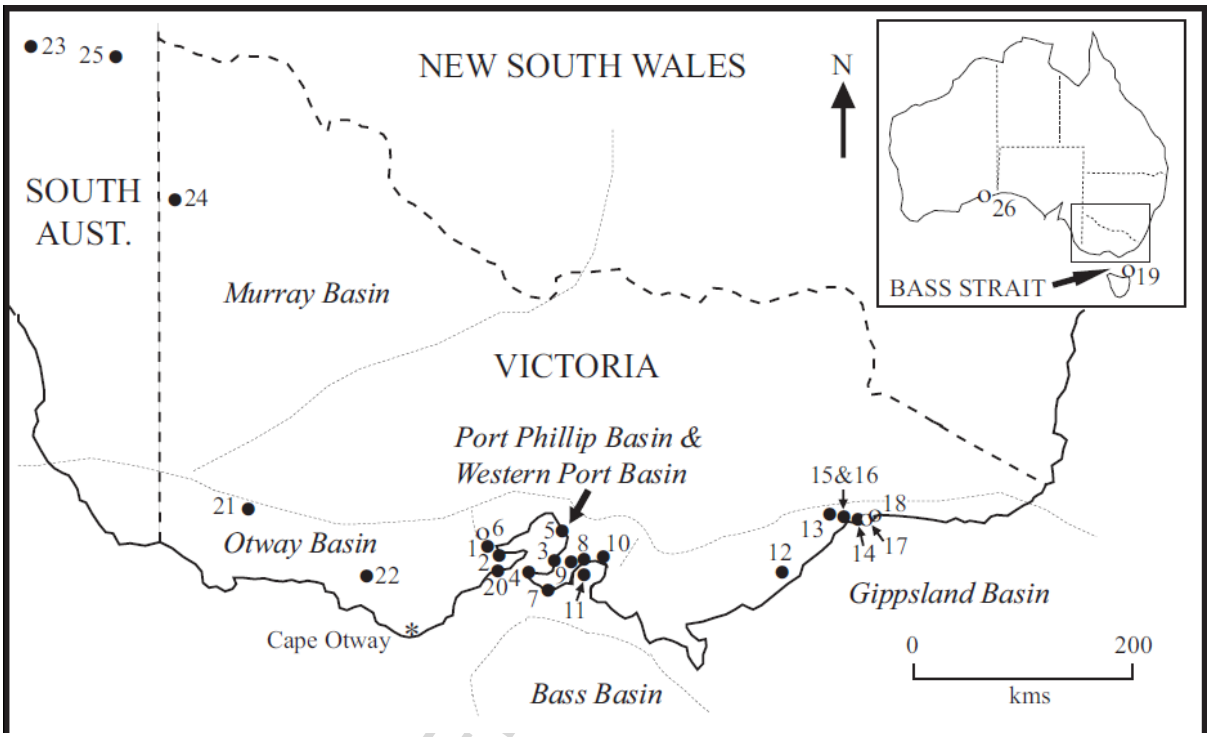


Fig. 2

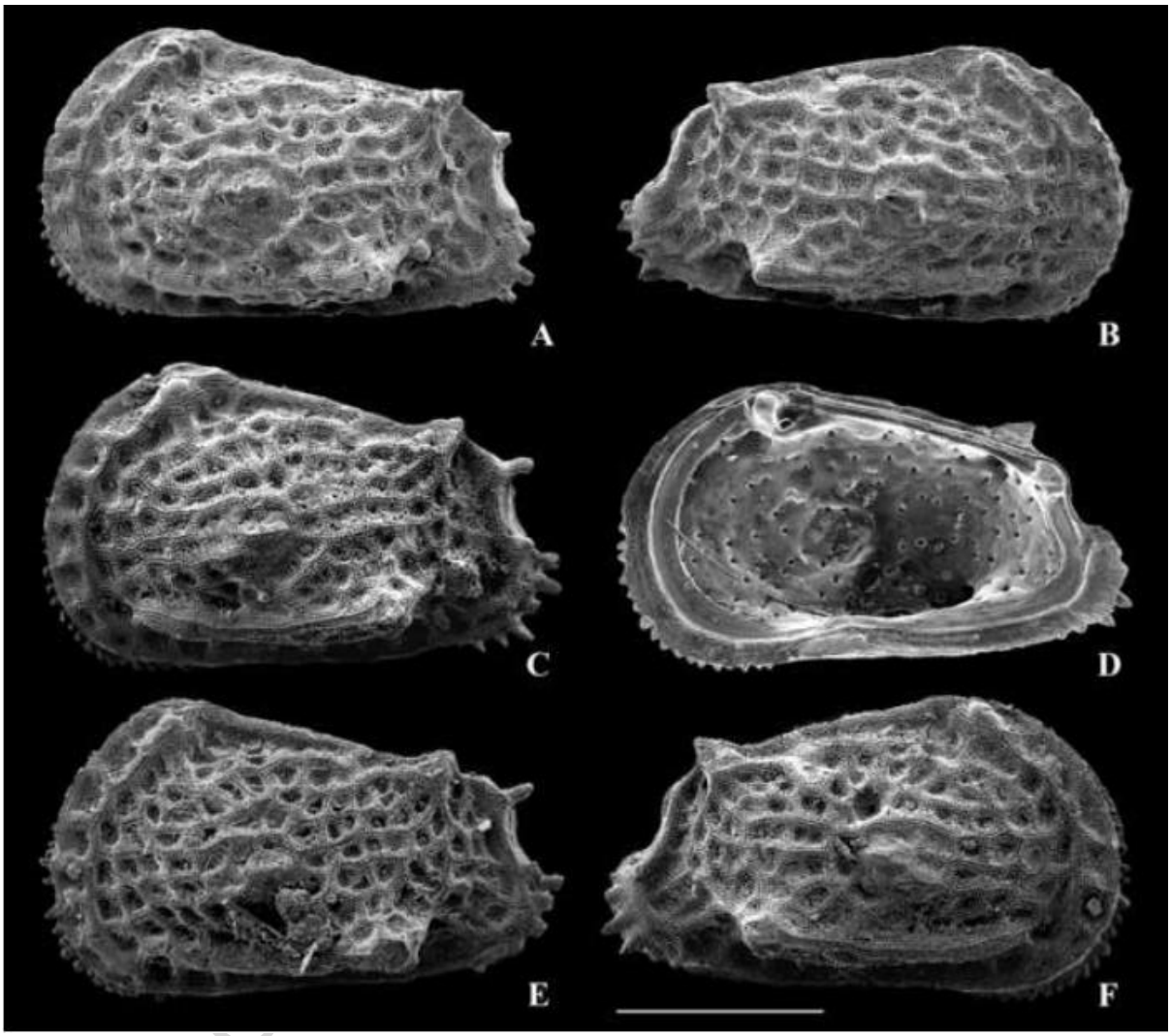


Fig. 3

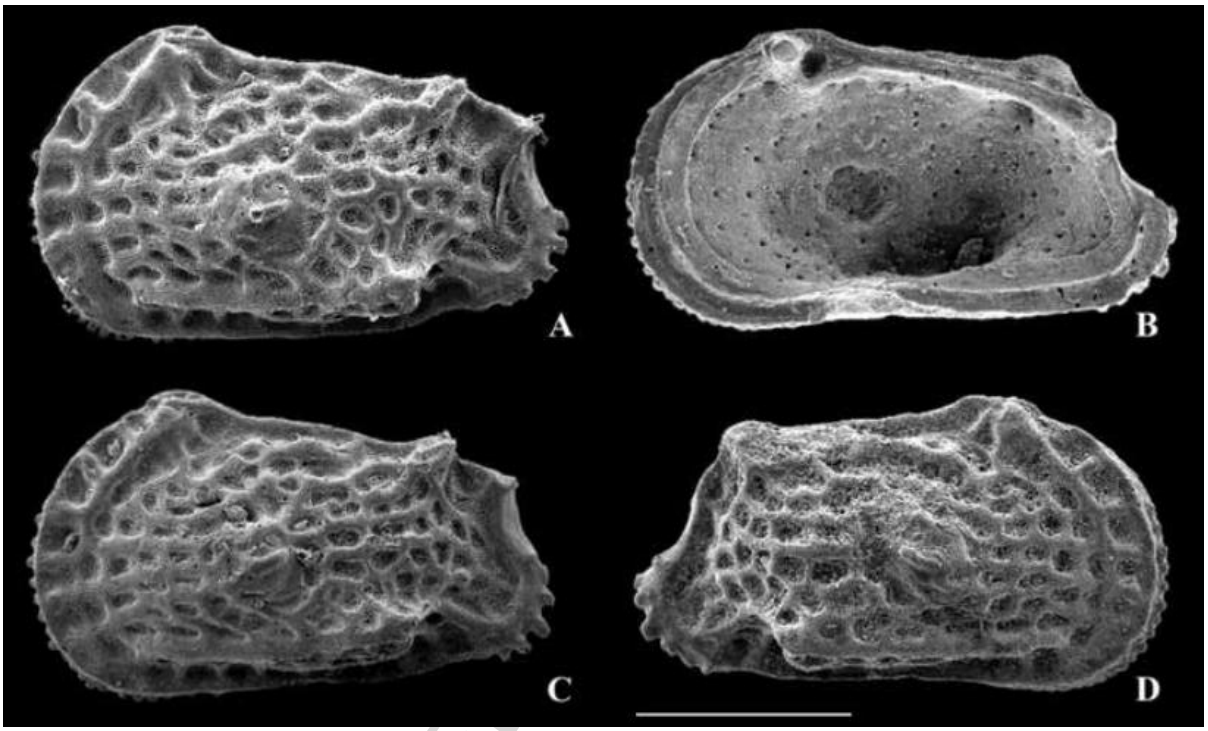


Fig. 4

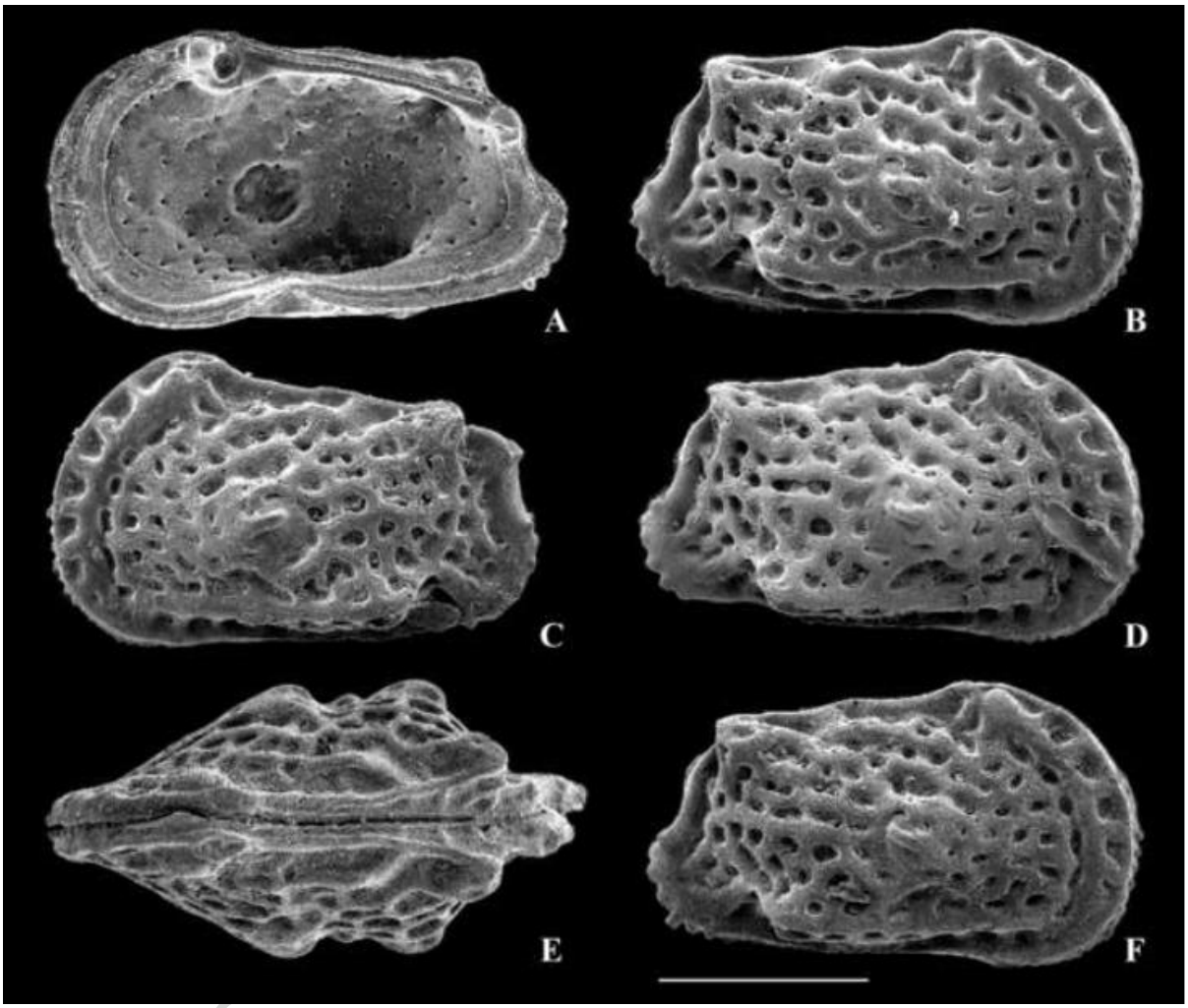


Fig. 5

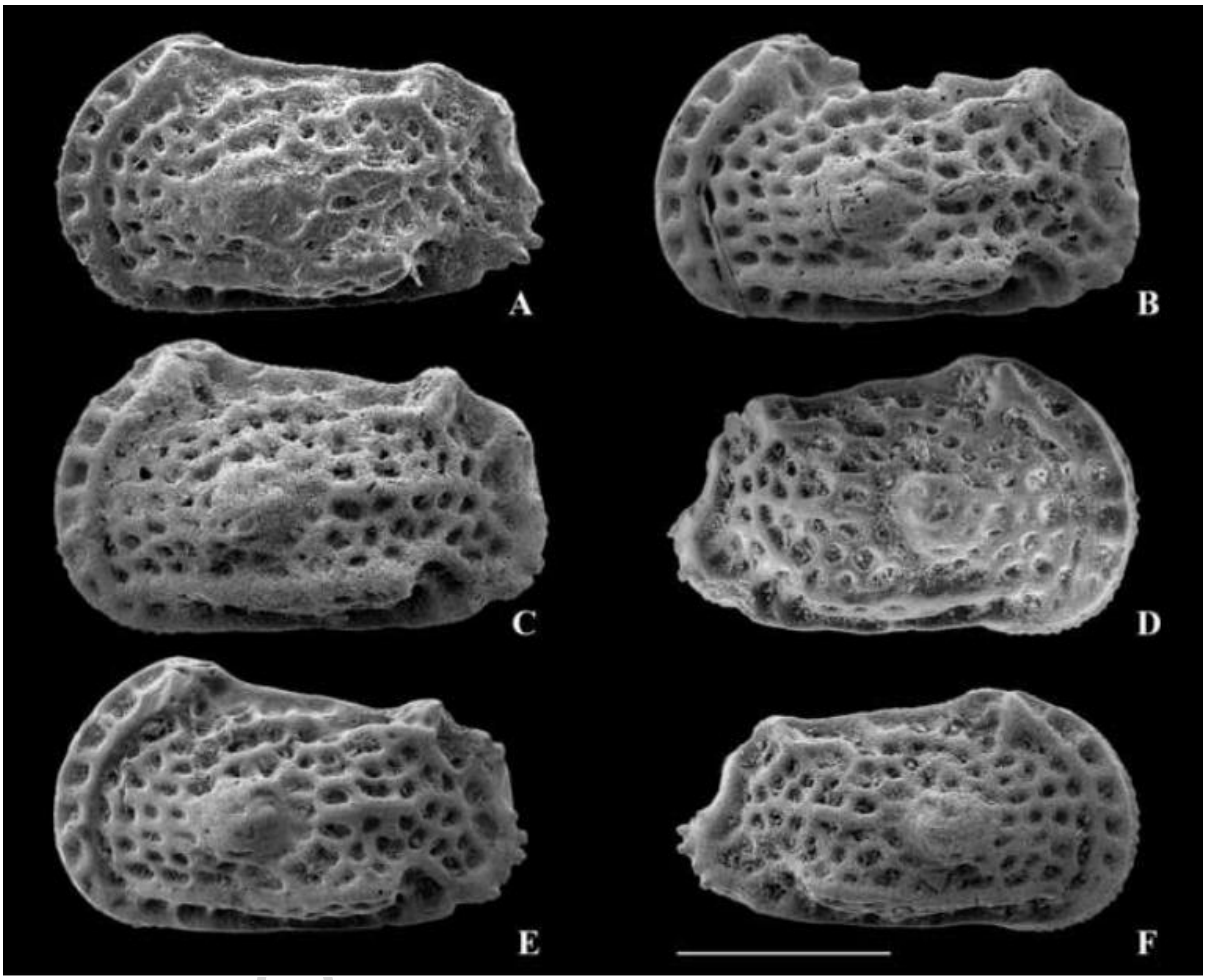


FIg. 6

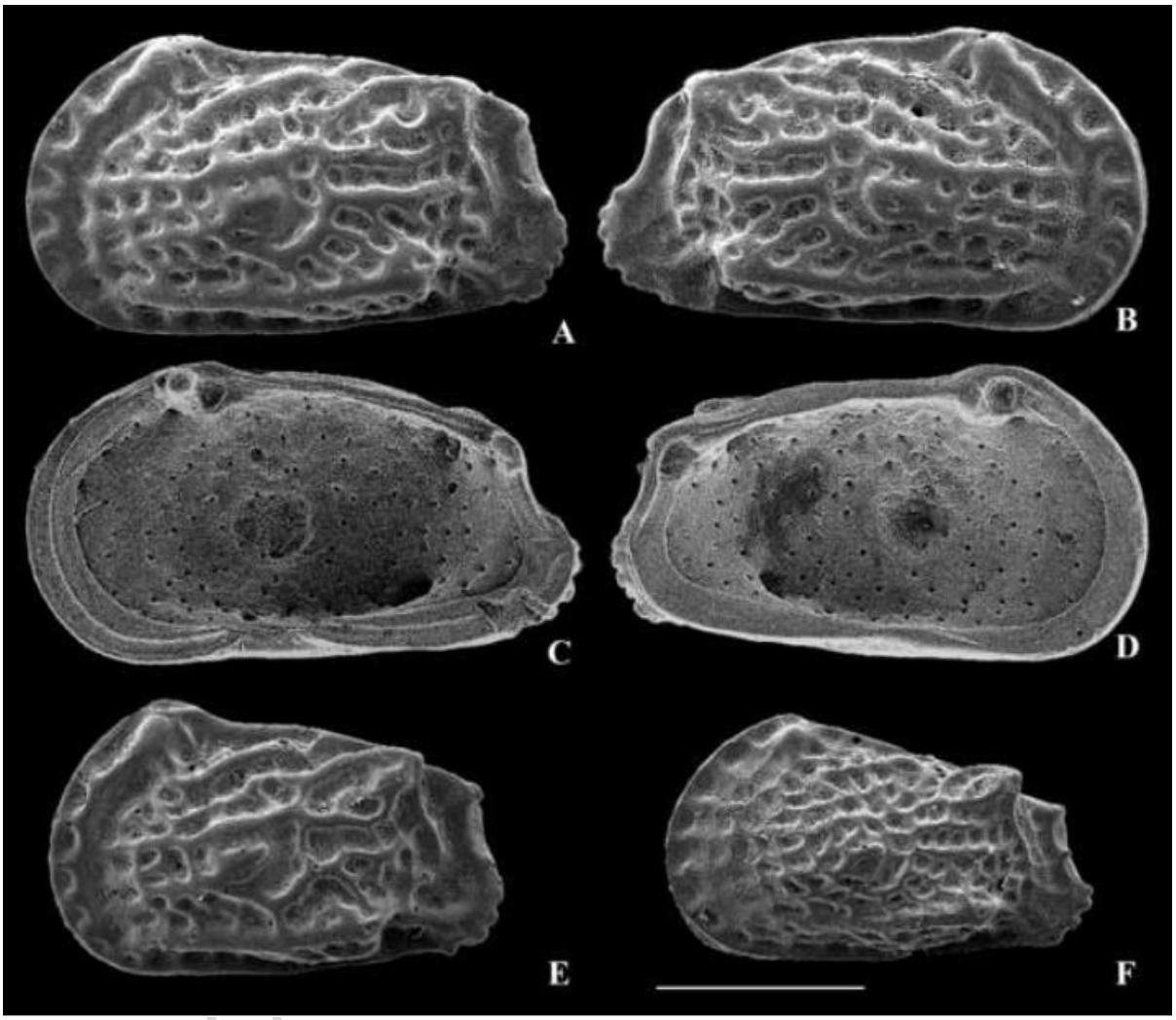


Fig. 7

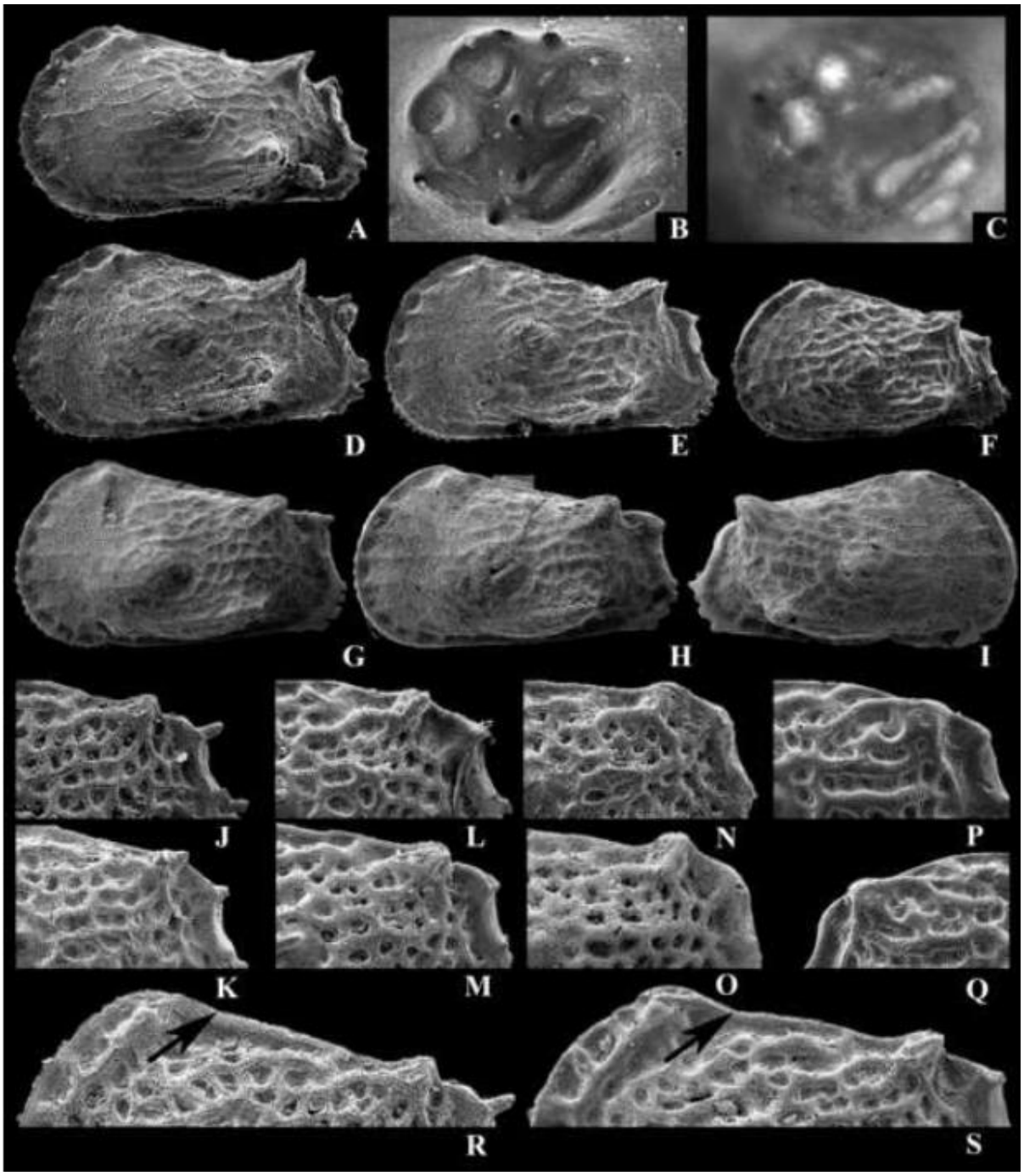


Fig. 8

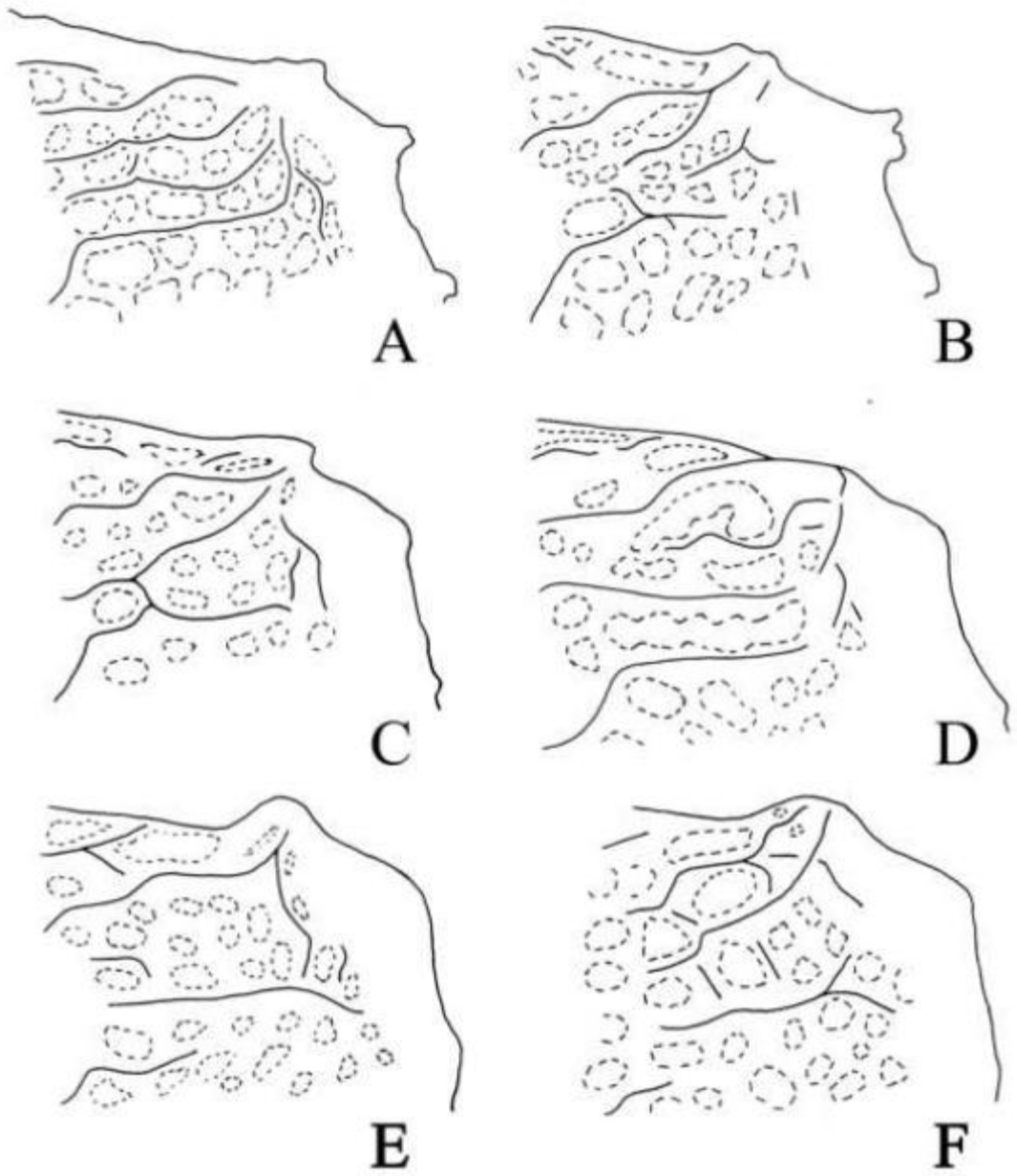


Fig. 9

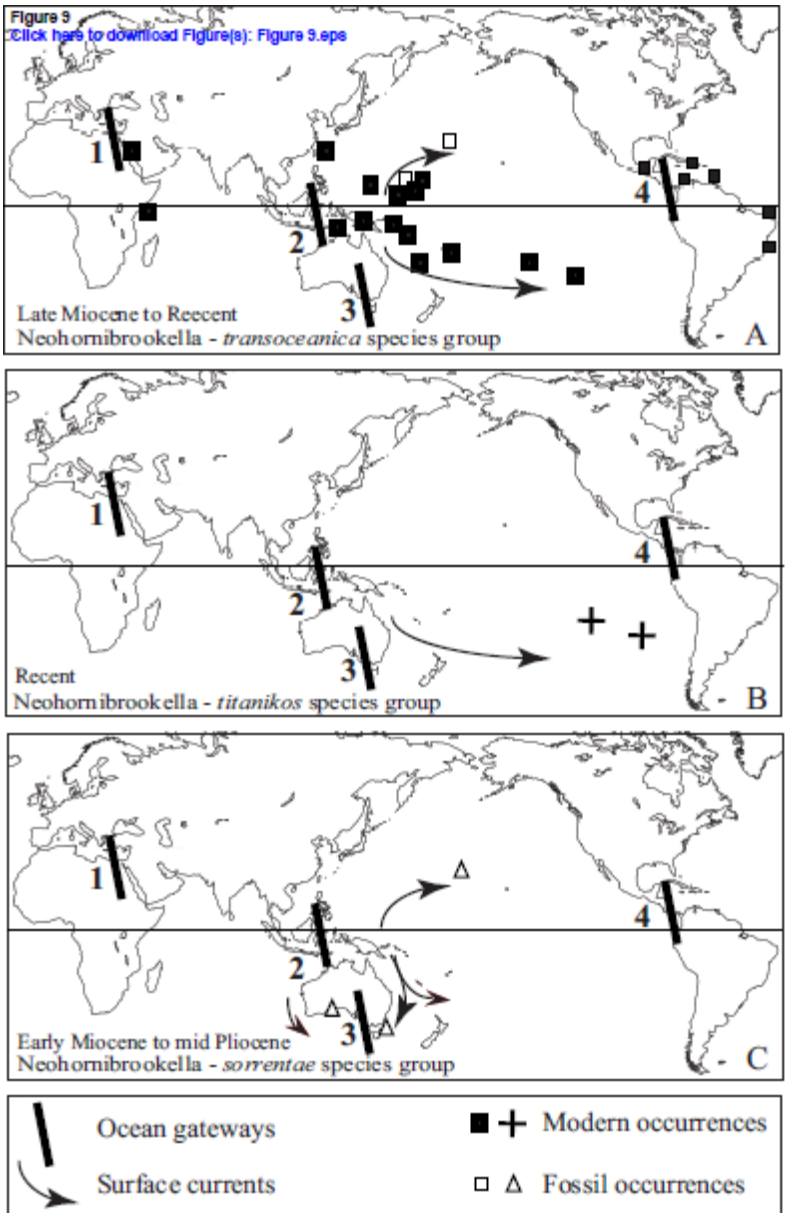


Fig. 10

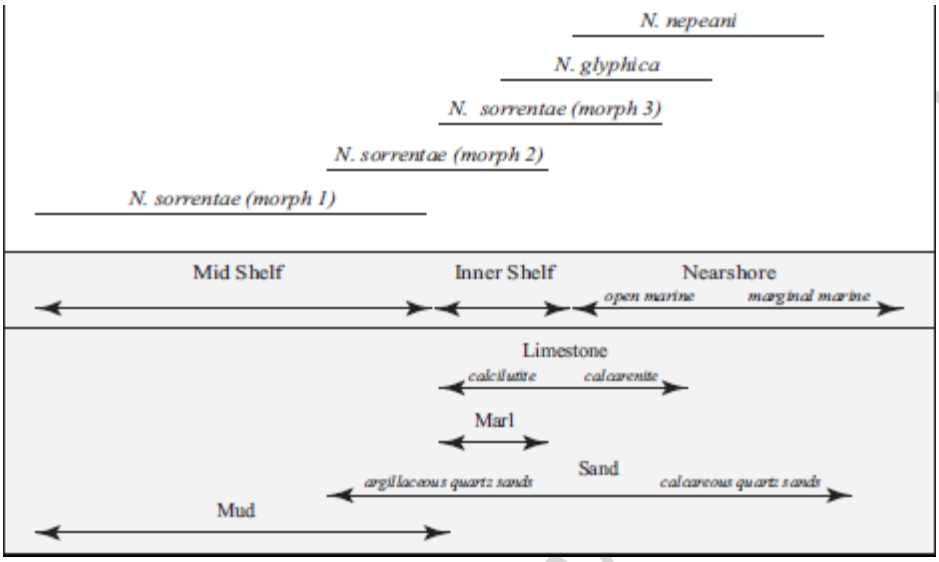


Fig. 11

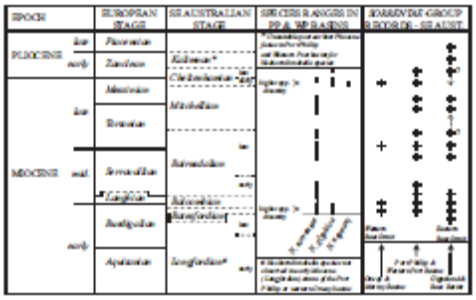
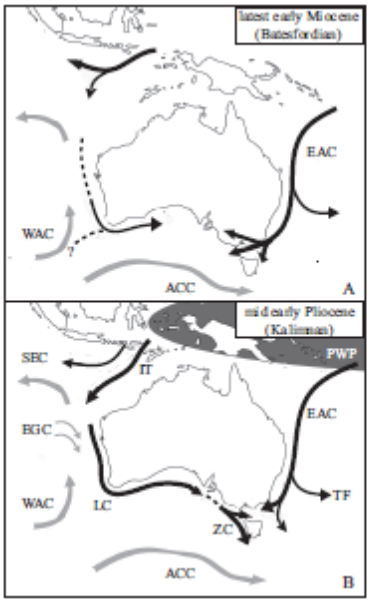


Fig. 12



Highlights

- Neohornibrookella, Tenedocythere and Bosasella systematic relationships.
- Neohornibrookella proxies of historical fluctuations in East Australian Current.
- Neogene marine palaeobiogeographical gateway in Bass Strait, southeast Australia.
- Palaeo-habitat specialisation of ostracod intraspecific morphotypes.
- Tenedocytherinae new subfamily